Vegetation patterns 25 years after the eruption of Mount St. Helens, Washington, USA[1]

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In 2004, we surveyed the vegetation on Mount St. Helens to document changes since 1992. We asked how communities differentiate and if they develop predictable relationships with local environments. We sought evidence from links between species and environment and changes in community structure in 271 250-m^2 plots. The habitats of the seven community types (CTs) overlapped broadly. Ordination methods demonstrated weak correlations among species distributions and location, elevation, and surface variables. Comparisons to 1992 by habitat demonstrated a large increase in plant cover and substantial development of vegetation structure. Pioneer species declined while mosses increased proportionately leading to more pronounced dominance hierarchies in most habitats. In *Lupinus* colonies, dominance declined, and diversity increased due to the increased abundance of formerly rare species. On once barren sites, dominance increased, but diversity changed slightly, which suggested the incipient development of competitive hierarchies. Weak correlations between vegetation and the environment suggested that initially stochastic establishment patterns had not yet been erased by deterministic factors. A vegetation mosaic that is loosely controlled by environmental factors may produce different successional trajectories that lead to alternative stable communities in similar habitats. This result has implications for restoration planning.

Key words: canonical correspondence analysis; detrended correspondence analysis; *Lupinus lepidus*; Mount St. Helens; primary succession; vegetation dynamics; vegetation structure.

Understanding how species invade new sites, interact with a developing environment and with other species, and forge communities during primary succession is a challenge. Early in this process, species establishment is largely stochastic (Økland, 1999; del Moral et al., 2005), but eventually, deterministic processes should produce predictable relationships between species and their environments. In this study, we relate vegetation patterns at Mount St. Helens to environmental factors following 25 years of primary succession. We compare structure to that described in 1992 (del Moral et al., 1995) when vegetation was sparse and heterogeneous and stochastic factors appeared to dominate establishment. Understanding vegetation assembly patterns can produce more effective vegetation restoration and management.

Mount St. Helens erupted in 1980 to form an extensive barren plain on its north face. Ecologists continue intensive study of this area, leading to improved understanding of successional mechanisms (Walker and del Moral, 2003). For example, del Moral and Ellis (2004) showed that dispersal was spatially constrained because the seed rain is sparse. The relationship between vegetation and environment in wetlands was weak (Titus et al., 1999) but strengthened over time (del Moral, 1999a, b). Bishop et al. (2005) reported how herbivory limits the spread of *Lupinus* and can alter the rate and direction of succession.

The study of species assembly has practical constraints. At best, small permanent plots are monitored (Roozen and Westhoff, 1985; Olff and Bakker, 1991; del Moral, 2004), often for only a few years. Chronosequences, in which differences in space are assumed to reflect temporal differences (Kitayama and Mueller-Dombois, 1995), can be misinterpreted (De Kovel et al., 2000; Martínez et al., 2001; Sýkora et al., 2004). However, chronosequence studies conducted on lavas in Hawaii (Clarkson, 1998) and Sicily (Poli Marchese and Grillo, 2000), where sites of different age are in close proximity, have produced convincing interpretations.

This broad vegetation survey on Mount St. Helens connects experimental studies (e.g., Fagan et al., 2004) concentrating on mechanisms to remote sensing studies (Lawrence, 2005) that describe landscape changes. While the latter demonstrates vegetation development, community structure cannot be discerned. We address three questions. (1) Has the vegetation differentiated sufficiently to define different community types (CTs)? For CTs to be valid vegetation must be homogeneous, dominated by a few species, and be related to either habitats or to some environmental factors. (2) Are species patterns closely tied to environmental patterns? Linkages between environmental factors imply the development of deterministic patterns, a step in the formation of communities. However, if species patterns are linked only to spatial factors or only weakly associated to any factor, then we conclude that stochastic factors continue to play a large role in determining the vegetation. (3) Does the vegetation show hierarchies of dominance? Since 1992, when stochastic factors appeared to dominate colonization patterns, surfaces have stabilized, fertility has increased, and vegetation cover has developed. If this development includes changes in dominance hierarchies, then we conclude that biological factors could produce vegetation that is more consistently tied to environmental factors.

MATERIALS AND METHODS

Study sites—The surfaces of the study area on Mount St. Helens originated on 18 May 1980 after a series of cataclysmic events that included the largest landslide in history, a directed blast that deposited deep pumice over the study area, and several large pyroclastic flows. Five more pyroclastic events seared this Pumice Plain in 1980 to form deposits over 40 m thick (Swanson and
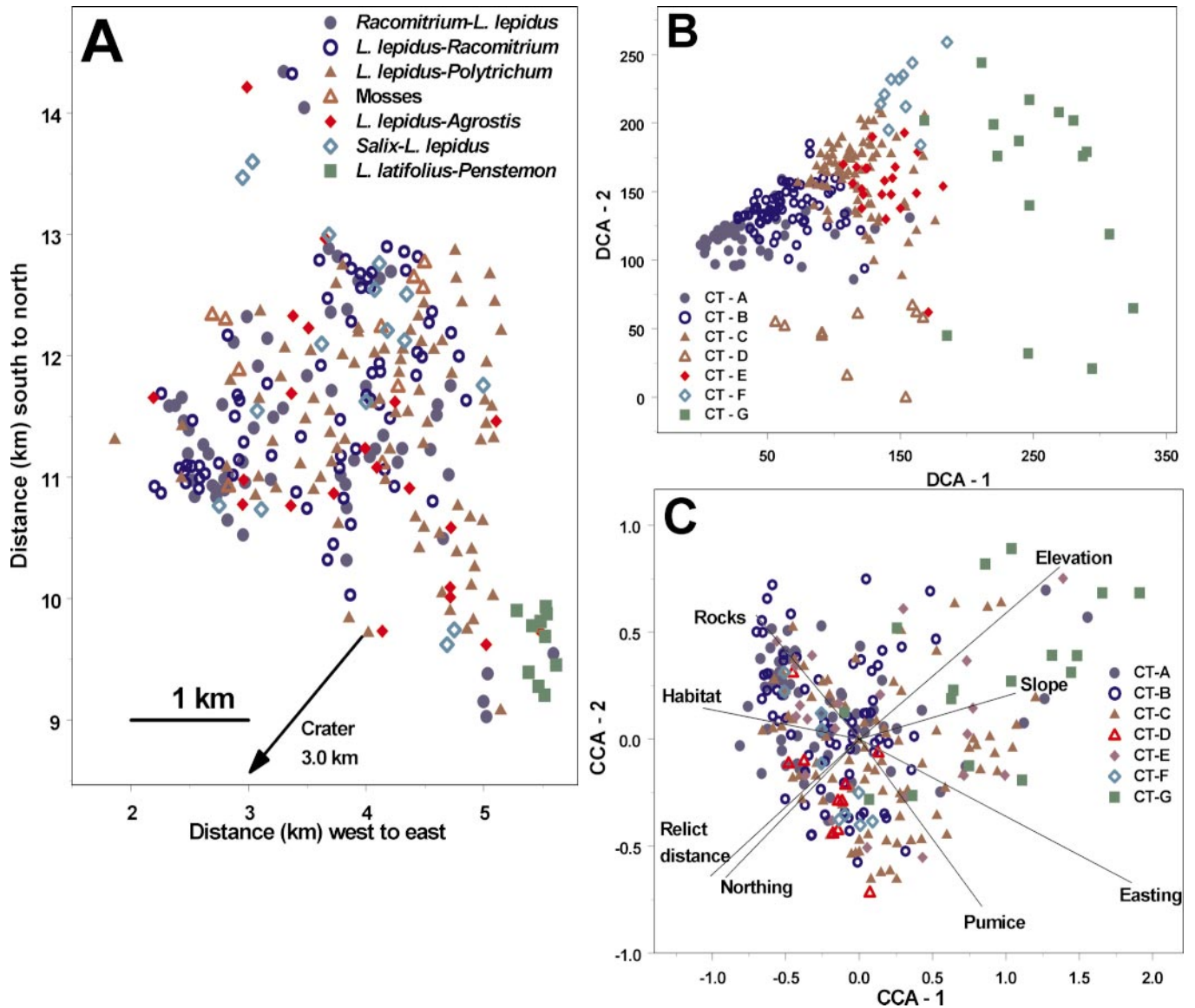
Fig. 1a.   Spatial distribution of plots on the Pumice Plain, Mount St. Helens, distinguished by community types. Distance west (UTM 56–1863 m E) to east (UTM 56–5614 m E) corresponds to the longitude, "Easting"; distance south (10 T 5 119 030 m N) to north (10 T 5 124 613 m N) corresponds to the latitude. The arrow indicates the direction and approximate distance to the center of the crater. The legend lists a descriptive name for each of the seven community types (*Racomitrium* = *R. canescens*; *Agrostis* is *A. pallens*; *Penstemon* is *P. cardwellii*; *Polytrichum* is *P. juniperinum*). Fig. 1b. Detrended correspondence analysis (DCA) ordination of plots on the Pumice Plain, Mount St. Helens, symbolized by community type (see Fig. 1a). Fig. 1c. Canonical correspondence analysis (CCA) ordination of plots on the Pumice Plain, Mount St. Helens, symbolized by community type (see Fig. 1a). Vectors were multiplied by five for better resolution. "Habitat" is either pumice or pyroclastic sites. "Pumice" is the percentage of pumice on the surface.

Major, 2005). The resultant landscape was devoid of vegetation and soil, except in a few "refugia," northeast of the crater (cf. Titus et al., 1998).

To describe the vegetation of recently formed upland substrates, we sampled 271 plots over about 13 km² north of the crater (Fig. 1a), on stable substrates between 1056–1387 m. Three surfaces were sampled. Pyroclastic ejecta, deposited north of the crater, have been eroded, leaving mixtures of old lava rocks and pumice with pockets of fine materials. Pumice ejected by the blast, by now weathered to gravel, was concentrated to the east and south of the study area. Melting snow subsequently created broad, rocky, unstable drainage channels. Erosion has deepened these channels to stabilize the adjacent surfaces (Wood and del Moral, 1988; Bishop et al., 2005).

Lupinus lepidus, a nitrogen-fixing species, is central to the vegetation dynamics of this region. It was the first species to colonize and the only vascular plant to produce dense clusters. In 1992, moderately dense vegetation could

only be found associated with such clusters, so del Moral et al. (1995) considered vegetation samples separately from the three habitat types. For comparisons to that study, plots with greater than 50% cover by *Lupinus* were considered to be "*Lupinus* colonies." None occurred on drainages, and those that occurred on either pyroclastic or pumice surfaces were not assigned to those categories.

Sampling—Plots were established in homogeneous sites with some vegetation. Approximate locations were determined *a priori* such that from 200 to 300 plots would be distributed within the study area. Approximate locations were determined by the global positioning system (GPS), then a central point was selected haphazardly within a homogeneous site. We excluded sites within 50 m of Spirit Lake, within 100 m of a previous plot, or disturbed by elk or by erosion, as well as wetlands and refugia. Vegetation was sampled by

TABLE 1. Cover of common species in each community type on the Pumice Plain, Mount St. Helens. *P* = significance level for ANOVA of cover; group sample size is in parentheses; superscripts unite members of homogeneous groups (Bonferroni comparisons, *P* < 0.05); tr = trace occurrence. Species with significant ANOVA, but no superscripts lacked differences by the Bonferroni test. Communities are listed in order of mean DCA-1 score.

Species	$P \leq$	Community type (CT)						
		A (62)	B (69)	C (83)	D (10)	E (21)	F (10)	G (16)
Racomitrium canescens	0.000	46.7[A]	32.2[B]	4.10[C]	14.2[BC]	1.41[C]	1.50[C]	2.45[C]
Cistanthe umbellata	0.03	0.36[A]	0.36[A]	0.31[AB]	0.02[B]	0.41[A]	0.03[B]	0.04[B]
Lupinus lepidus	0.000	11.3[B]	26.7[A]	28.1[A]	9.67[B]	8.87[B]	8.91[B]	0.66[C]
Hieracium albiflorum	0.006	0.45[B]	0.70[AB]	0.48[B]	1.17[A]	0.34[B]	0.50[AB]	0.37[B]
Agrostis scabra	0.05	0.73	0.63	0.87	0.39	1.53	0.42	0.19
Elymus elymoides	0.001	0.03[B]	0.05[B]	0.04[B]	0.56[A]	0.19[AB]	0.0[B]	0.0[B]
Polytrichum juniperinum	0.000	0.82[C]	2.16[BC]	3.6[B]	22.4[A]	0.73[C]	0.52[C]	0.75[C]
Hypochaeris radicata	0.000	1.27[B]	2.03[AB]	1.00[B]	10.5[A]	0.67[B]	0.56[B]	1.57[B]
Salix commutata	0.000	0.62[B]	0.96[B]	1.26[B]	0.38[B]	0.42[B]	9.56[A]	0.34[B]
Epilobium spp.[a]	0.000	0.02[B]	0.06[B]	0.06[B]	5.03[A]	0.02[B]	0.03[B]	0.05[B]
Anaphalis margaritacea	0.000	0.28[BC]	0.25[C]	0.21[B]	1.14[A]	0.29[B]	0.44[B]	0.96[A]
Castilleja miniata	0.01	0.20[B]	0.65[AB]	1.30[AB]	2.56[A]	0.16[B]	1.63[AB]	1.94[A]
Carex mertensii	0.02	0.19[B]	0.22[B]	0.35[AB]	0.16[B]	0.23[B]	0.41[AB]	0.87[A]
Achillea millefolium	0.05	0.08	0.10	0.20	0.87	0.52	0.6	0.80
Grimmia sp.	0.01	0.15[B]	0.51[B]	0.30[B]	0.82[AB]	0.11[B]	2.60[A]	2.48[A]
Agrostis pallens	0.000	0.08[B]	0.20[B]	1.39[A]	1.38[AB]	1.94[A]	0.18[B]	2.58[A]
Penstemon sericea	0.04	0.03	0.34	0.03	0.20	0.32	0.0	0.28
Phacelia hastata	0.04	0.02	0.20	0.05	0.0	0.16	0.0	0.17
Chamerion angustifolium	0.001	0.06[B]	0.07[B]	0.08[B]	0.06[B]	0.04[B]	0.08[B]	0.35[A]
Alnus viridus	0.001	tr[B]	0.07[B]	0.35[B]	0.0[B]	0.07[B]	0.14[B]	1.74[A]
Penstemon cardwellii	0.000	0.40[B]	0.54[B]	0.82[B]	0.08[B]	0.65[B]	0.04[B]	6.37[A]
Carex microptera	0.000	tr[B]	0.01[B]	0.04[B]	tr[B]	0.05[B]	0.0[B]	0.51[A]
Carex paysonis	0.000	tr[B]	tr[B]	0.04[B]	0.0[B]	tr[B]	tr[B]	0.29[A]
Saxifraga ferruginea	0.000	0.02[B]	0.02[B]	0.15[B]	0.0[B]	0.07[B]	0.0[B]	1.25[A]
Luzula parviflora	0.000	0.02[B]	0.20[B]	0.04[B]	0.0[B]	tr[B]	0.0[B]	0.48[A]
Lupinus latifolius	0.000	0.38[B]	0.04[B]	0.24[B]	0.0[B]	1.13[B]	0.0[B]	23.0[A]

[a] *Epilobium* spp. includes *E. anagallidifolium* and the closely related *E. paniculatum*.

determining cover in 12 1-m² quadrats per 250-m² circular plot, arrayed on four 9-m radii 2, 4, and 6 m from the center. Species present in a plot but not in a quadrat were assigned a score of 0.01%.

Geographic and geomorphic features were determined. Locations relative to refugia and wetlands were scored as: 1 = <20 m; 2 = 20–50 m; 3 = >50 m. Del Moral and Eckert (2005) showed that biologically rich sites have little impact beyond 20 m. Aspect was determined by compass and indexed to reflect increasing insolation: 1 = 0–45° and 330°–360°; 2 = 46°–80° and 280°–329°; 3 = 81°–115° and 245°–279°; 4 = 114°–135° and 210°–244°; 5 = 134°–209°. Slope was determined by inclinometer and converted to a five-part scale: 1 = 0–5° to 5 = over 21° in 5° increments. Exposure was determined as follows: 1 = ravines or bottom of slope, 2 = shielded from wind or north facing, 3 = gentle slopes open to some wind, 4 = exposed to wind, and 5 = ridges. The elevation was determined by plotting GPS coordinates on the U.S. Geological Survey (USGS) digital map. The habitat (pumice or pyroclastic area) was determined from the impact map (Swanson and Major, 2005). Habitat type and the presence or absence of rills and drainage courses were noted. Surface texture was estimated visually to the nearest 5% for rocks (>2 cm), gravel (0.5–2.0 cm), sand (<0.5 cm), and fines. The surface type (percentage cover of pumice) was estimated visually for the plot. Species nomenclature follows the Integrated Taxonomic Information System (ITIS) as shown on the Mount St. Helens website (del Moral, 2004).

Data summary—The number of species (richness, *S*) and the species percentage cover were summarized and used to calculate the Shannon index ($H' = -\Sigma p_i \ln p_i$), the complement of Simpson's dominance index [$D = (1 - \Sigma p_i^2)$], and evenness [$E = H'/\ln(\text{richness})$]. *D* and *E* vary from 0–1. Each index depends on p_i, the proportion of the cover represented by species *i* (McCune and Mefford, 1999).

Floristic analyses—To facilitate descriptions, plots were classified into floristic groups using flexible sorting (ß = −0.25) with Euclidean distance. Clus-

ters were determined from the dendrogram. Multiresponse permutation procedures (MRPP; McCune and Grace, 2002) were applied to assess the validity of the classification.

Nonmetric multidimensional scaling was used to determine the number of effective dimensions in the floristic data, but its result was no better than a detrended correspondence analysis (DCA; McCune and Grace, 2002). Because DCA provides scaling in floristic units, we used this method. All ordinations were conducted using PC-ORD (McCune and Mefford, 1999).

Statistical analyses—One-way analysis of variance (ANOVA) followed by Bonferroni tests of differences among the means were used to compare means of several groups.

RESULTS

Community types—Cluster analysis produced seven community types (CT) that were significantly different from each other (MRPP). The chance-corrected, within-group agreement, **A**, was only 0.08 (*P* < 0.0001), indicating distinct, but variable, groups (*t* = −14.9). All pairwise comparisons were significant. There were 16 common species (cover >1%) and 10 additional ones with significant cover differences among the CTs (Table 1). Species with ANOVA probabilities close to 0.05 did not show differences among the CTs. The distribution of the CTs was weakly correlated to geographic position (Fig. 1a). The habitat variables were compared by ANOVA. The CTs did not differ with respect to aspect, exposure, distance to wetlands, or percentage of sandy surfaces, but they were correlated to habitat features that were spatially based. We ranked each variable from 1 to 7 and recorded only the rank of each CT to facilitate comparisons (Table 2).

TABLE 2.   Environmental factors for which community types on the Pumice Plain, Mount St. Helens, differed. Environmental factors are ranked from 1–7 rather than their actual values to highlight patterns. P = ANOVA significance for the comparison; superscripts indicate membership in homogeneous groups. Lack of a subscript indicates no differences by the Bonferroni test. Sample size is in parentheses.

Parameter	Type	$P \leq$	Community type (CT)						
			A (62)	B (69)	C (83)	D (10)	E (21)	F (10)	G (16)
Easting	West→east	0.000	1^A	2^A	6^B	4^{AB}	5^{AB}	3^{AB}	7^C
Northing	North→south	0.000	4^A	3^A	5^A	2^A	6^{AB}	1^A	7^A
Elevation	Low→high	0.000	4^{AB}	3^{AB}	5^{AB}	2^A	6^B	1^A	7^C
Slope	Shallow→steep	0.02	3^B	5^B	6^B	2^A	4^B	1^A	7^B
Relict proximity	Near→distant	0.003	4^A	3^A	5^A	2^A	6^{AB}	1^A	7^B
Gravel	Low→high	0.001	6^B	3^B	5^B	4^B	7^B	1^A	2^A
Rock	Low→high	0.01	7^B	6^B	4^{AB}	5^{AB}	3^{AB}	2^{AB}	1^A
Rills	Rare→common	0.007	4^{AB}	6^{AB}	7^B	1^A	5^{AB}	2^A	3^{AB}
Pyroclastic	Low→high	0.000	5^B	4^B	3^A	6^B	2^A	7^B	1^A

Racomitrium canescens–Lupinus lepidus (CT-A)—CT-A was widely distributed and included several species with good wind dispersal; *Hypochaeris*, *Hieracium*, *Anaphalis*, and *A. scabra*, were common. CT-A was exceptional only in being the rockiest type.

Lupinus lepidus–Racomitrium canescens (CT-B)—CT-B was environmentally similar to CT-A, and overlapped it spatially. Erosion was more evident and rills prominent. Several wind-dispersed pioneer species, *Salix*, *Carex* spp., and *Penstemon* spp. were frequent.

Lupinus lepidus–mosses (CT-C)—CT-C was nearly ubiquitous, being scattered throughout the study area. *Lupinus lepidus* cover peaked in this type, while *Racomitrium* and *Polytrichum* were characteristic. *Agrostis* spp., *Penstemon cardwellii*, and *Castilleja* were frequent. Rills were common and slopes were relatively steep.

Polytrichum juniperinum–Racomitrium canescens (CT-D)—CT-D was also characterized by *L. lepidus*, *Hypochaeris*, *Castilleja*, and *Epilobium* spp., suggesting that these sites were more fertile than were others. Plots were at low elevations on gentle pyroclastic surfaces. Though rocks were frequent, erosion appeared to be limited.

Lupinus lepidus–Agrostis spp. (CT-E)—CT-E was relatively barren; *Racomitrium* was the only other frequent species. This CT typically occurred on pumice at higher elevations with rocky surfaces and frequent rills.

Salix commutata–Lupinus lepidus (CT-F)—In addition to the characteristic species, only *Castilleja* and mosses occurred frequently in CT-F. It was environmentally similar to CT-D and found primarily on the gentlest slopes on pyroclastic sites close to Spirit Lake.

Lupinus latifolius–Penstemon cardwellii (CT-G)—CT-G was dominated by species that may have survived in the relicts found near many of these plots. *Alnus viridus* was relatively common, as were *Agrostis pallens*, *Hypochaeris*, and *Saxifraga*. It occupied the steepest sites and was concentrated on the highest slopes in the northeast of the study area.

Structure—The CTs differed in all structural measure (Table 3). The survey sampled all widespread and common species listed by Titus et al. (1998), as well as most of the infrequent ones. Total richness was weakly correlated to sample size and showed no consistent patterns. Mean species richness generally increased from CT-A, dominated by *Racomitrium*, to CT-G, which was adjacent to refugia.

Total cover was greatest where mosses were dominant and *Lupinus* common (CT-A, CT-B), and least in CT-E and CT-F where mosses were infrequent and *L. lepidus* less common.

Diversity (H') tended to increase from CT-A to CT-G, which is related to the DCA-1 axis. There was strong dominance by mosses and *Lupinus lepidus* where diversity was low, while no species predominates where diversity was high. Floristic variation within each CT was large, so that H' overlapped greatly and were variable, features not representative of an integrated community.

Patterns in *E* and *D* differed in their details, but followed those of diversity. Both peaked in CT-E, where cover was least. These equitability measures were least in CT-A, where *Racomitrium* dominated and *L. lepidus* was common. These measures were relatively low in CT-B and CT-C, where mosses and *L. lepidus* dominated.

Plot distribution—The plots were assigned to one of four habitat categories: pumice, pyroclastic, drainage, and dense *Lupinus* (>50% cover) for comparisons to the 1992 study (see **Comparison to 1992**). The χ^2 test of the seven CT by four habitat types demonstrated a significant relationship (χ^2 =

TABLE 3.   Structural features of community types on the Pumice Plain, Mount St. Helens. Statistics as in Table 1.

Structural measure	$P \leq$	Community type (CT)						
		A (62)	B (69)	C (83)	D (10)	E (21)	F (10)	G (16)
Total richness (S)	—	60	55	55	43	44	33	64
Species richness	0.002	15.0^A	16.5^{AB}	16.0^A	17.4^{AB}	15.0^A	16.4^{AB}	19.7^B
Percent cover	0.000	65.3^C	70.2^C	47.7^{BC}	77.1^C	21.9^A	29.1^{AB}	54.7^{BC}
Diversity (H')	0.000	1.02^A	1.34^B	1.35^B	1.57^{BC}	1.79^C	1.65^{BC}	1.69^C
Evenness (E)	0.000	0.379^A	0.482^B	0.492^{BC}	0.547^{BC}	0.671^D	0.615^{CD}	0.576^{BCD}
Dominance (D)	0.000	0.468^A	0.638^{BC}	0.573^B	0.700^{BCD}	0.751^D	0.710^{CD}	0.684^{BCD}

TABLE 4. Detrended correspondence analysis (DCA) scores for community types on the Pumice Plain, Mount St. Helens. Statistics as in Table 1, based on DCA scores. SD = standard deviation. See Fig. 1b.

Axis, SD	$P \leq$	Community type						
		A (62)	B (69)	C (83)	D (10)	E (21)	F (10)	G (16)
DCA-1	0.0000	36.1[A]	65.5[B]	117.4[C]	117.8[C]	138.4[C]	152.1[D]	254.2[E]
SD	—	32.7	22.8	21.9	36.6	20.0	14.9	47.9
DCA-2	0.0000	119.5[B]	137.8[C]	163.0[D]	46.3[A]	154.4[CD]	222.8[E]	150.8[CD]
SD	—	13.2	15.5	24.8	21.6	26.6	22.5	72.1

64.7; $P < 0.0001$), but each CT was distributed in at least two habitats and none had a strong affinity to any surface. CT-A was proportionally distributed in each habitat except that it lacked *Lupinus* colonies. CT-B was widely distributed, but slightly more frequently on pyroclastic and less so in drainages. CT-C was widely distributed in each habitat. CT-D lacked *Lupinus* colonies, but otherwise showed no surface preferences. CT-E and CT-G were concentrated on pumice and drainages, while CT-F was concentrated on pyroclastics and drainages. *Lupinus* colonies were largely assigned to CT-C, with a few in CT-B.

Indirect ordination—The DCA position of plots within each CT revealed much floristic variation (Fig. 1b). Variation on DCA-1 was 2.5 times that of DCA-2. DCA scores for each CT were compared by ANOVA (Table 4), and they differed strongly on each axis. On DCA-1, CT-C, CT-D, and CT-E formed a central group that overlapped, but the other CTs were unique. CT-D was distinguished from CT-C and CT-E on DCA-2, while CT-C and CT-E differed on DCA-3.

Stepwise regression of environmental variables vs. DCA-1 indicated correlations with easting ($+$; $P < 0.0001$), elevation ($+$; $P < 0.0001$), exposure ($-$; $P < 0.02$), rocks ($-$; $P < 0.03$), gravel ($-$; 0.04), and fines ($+$; 0.05), these variables collectively having $r^2 = 0.350$. The analysis of DCA-2 indicated correlations with elevation ($+$; $P < 0.006$), pumice ($+$; $P < 0.01$), and distance to wetland ($-$; $P < 0.05$), these variables having $r^2 = 0.063$.

The distributions of many common species were correlated to the first axis. *Racomitrium* was strongly negatively correlated and *L. lepidus* weakly so. Species abundant in CT-G increased with DCA-1 score (e.g., *Lupinus latifolius*, *Penstemon cardwellii*, *Saxifraga*, and *Castilleja*). Many species were negatively correlated to DCA-2. These included the pioneer

TABLE 5. Canonical correspondence analysis for vegetation on the Pumice Plain, Mount St. Helens. Significant canonical correlations for the multiple regression are in bold; other values differed between the community types but were not significant in the regression. CCA-1 = first canonical axis; CCA-2 = second canonical axis.

Parameter	CCA-1	CCA-2
Easting	**0.807**	−0.407
Northing	**−0.379**	−0.392
Elevation	**0.567**	0.490
Slope	**0.442**	0.130
Relict proximity	**−0.421**	−0.338
Pumice	**0.348**	−0.475
Gravel	−0.041	−0.025
Rocks	**−0.299**	0.352
Rills	−0.079	−0.100
Habitat type	**−0.443**	0.089

species *Hypochaeris*, *Hieracium*, and *Chamerion*, as well as *Achillea*. Both common mosses were strongly negatively distributed with respect to DCA-2, while *Carex paysonis* and *P. cardwellii* were positively correlated.

Direct ordination—CCA was applied to determine if the measured factors could predict species patterns. The plots were analyzed using 41 species that occurred in at least nine plots. Because variables rocks, gravel, sand, and fines totaled to 100%, we excluded sand a priori to reduce autocorrelations that render the analysis problematic (McCune and Grace, 2002).

Of the total variance, 7.4%, 3.5%, and 1.9% were associated with the first three axes, respectively. Pearson correlations between species and environment were low, 0.662, 0.561, and 0.458, respectively. Such low correlations suggest that stochastic factors remain important and that other factors might be operating at a scale smaller than that measured. However, both the eigenvalues and the correlations were significant (compared to 100 random simulations) and should be examined.

Of the 15 variables, only eight improved the fit when added to the regression. We interpret these results with caution and view them as hypotheses not explanations. Variables with the strongest correlations are shown as vectors that indicate their relative strengths. Plot locations, determined from the linear combination of environmental variables, are superimposed (Fig. 1c) to illuminate the environment to plot relationship.

Position effects were strong (Table 5). Easting had the strongest influence on CCA-1 and was significant on CCA-2. Elevation, strongly correlated to northing, was the second strongest factor on CCA-1 and the strongest factor on CCA-2. Similarly, slope increased with elevation and decreased with northing, so this factor was significant. Distance from relicts was significant on CCA-1. The degree of pumice-covered surface was the only significant factor on CCA-1 that was not spatially related. On CCA-2, slope, pumice, and easting were the leading variables. The percentage of the surface covered by rocks was the only significant local feature.

The plots were only weakly correlated to the canonical axes, and CTs did not cluster strongly (Fig. 1c). Because <13% of the vegetation variation was explained, this is not surprising. Species patterns with relationship to the CCA axes were explored with a linear regression model that combined first and second order terms for CCA-1 and CCA-2. Sixteen of 40 species had $r^2 > 0.10$ (mean = 0.31). The best relationships were *Lupinus latifolius* ($r^2 = 0.64$), *Racomitrium* ($r^2 = 0.63$), *Saxifraga* ($r^2 = 0.60$), *Epilobium* spp. ($r^2 = 0.52$), and *Penstemon cardwellii* ($r^2 = 0.45$).

Comparison to 1992—Sampling protocols in 1992 differed from the 2004 study. In 1992, the 141 plots were 100 m², but

TABLE 6. Structure comparisons for vegetation surveys conducted on the Pumice Plain, Mount St. Helens, in 1992 and in 2004. Total richness is all species encountered. Superscripts within a column of a group indicate membership in homogeneous groups (Bonferroni comparisons, $P < 0.05$). Contrasts between sample years were made with a simple t test with P shown in the last column. Richness in habitat types reported for all species (those with two or more occurrences). NA = not appropriate; NS = not significant.

Parameter	Habitat type[a]	1992	2004	$P \le$
Total richness	All sites	79	105	NA
Total richness	*Lupinus* colonies	52 (38)	44 (31)	NA
	Pumice	66 (50)	69 (54)	NA
	Pyroclastic	36 (26)	63 (49)	NA
	Drainages	42 (35)	68 (43)	NA
Mean richness	*Lupinus* colonies	12.5	17.1^A	0.02
	Pumice	11.7	17.0^A	0.0000
	Pyroclastic	9.8	15.3^B	0.0000
	Drainages	11.2	15.2^B	0.0006
Percent cover	*Lupinus* colonies	68.6^A	107.3^A	0.0001
	Pumice	7.2^B	56.8^B	0.0000
	Pyroclastic	2.9^B	56.5^B	0.0000
	Drainages	2.6^B	38.3^C	0.0000
Diversity (H')	*Lupinus* colonies	0.668^A	1.099^B	0.007
	Pumice	1.466^B	1.447^A	NS
	Pyroclastic	1.443^B	1.228^B	0.05
	Drainages	1.503^B	1.398^{AB}	NS
Evenness (E)	*Lupinus* colonies	0.254^A	0.384^A	0.03
	Pumice	0.610^B	0.515^B	0.0005
	Pyroclastic	0.644^B	0.455^C	0.0000
	Drainages	0.629^B	0.518^B	0.01
Dominance (D)	*Lupinus* colonies	0.301^A	0.512^C	0.005
	Pumice	0.646^B	0.627^B	NS
	Pyroclastic	0.654^B	0.563^A	0.03
	Drainages	0.637^B	0.600^{AB}	NS

[a] Sample sizes: *Lupinus* sites 19 (1992) and 17 (2004) plots; pumice, 49 and 117 plots; pyroclastic 17 and 84 plots; drainages 21 and 53 plots.

the cover of all species in the plot with <5% cover was measured directly. Otherwise, visual estimates were used. GPS technology was unavailable, so locations were approximate. Sampling in both years appeared to cover the range of floristic variation and in each year only sites with vegetation were selected for sampling. In 1992, 1.41 ha were sampled, while in 2004, 6.775 ha were sampled across approximately the same area. In both years, sampling was representative, if not comprehensive.

Vegetation structure—Total richness increased from 79 to 105 species (Table 6). Richness within *Lupinus* colonies declined, while richness on pumice was comparable. Pyroclastic and drainage areas both produced a substantial increase in species richness.

In 1992, mean richness per plot in the four habitats did not differ significantly. By 2004, there were significant differences among habitats, and each habitat had increased richness. In 1992, cover in *Lupinus* colonies was more than 10 times other habitats. By 2004, they were denser still, largely from increased moss cover, but cover in the other types had increased markedly. Drainage surfaces have stabilized, with erosion being increasingly confined to stream channels. This has allowed vegetation to develop on once unstable surfaces.

Diversity (H') increased in *Lupinus* colonies as more species invaded and *L. lepidus* dominance declined. In contrast, on pyroclastic sites a few species achieved dominance. On pum-

ice and in drainages increases in richness were countered by greater dominance so that in 2004 H' did not differ from 1992.

E and D demonstrated strong dominance in *Lupinus* colonies but greater equitability elsewhere. By 2004, *Lupinus* colonies were more diverse and *Lupinus* less dominant. In contrast, dominance was more pronounced on the other sites, thus reducing equitability. Dominant species varied, but included mosses, *Agrostis* spp., and *Penstemon cardwellii*. In 2004, there remained significant differences among the sites in these measures (Table 6). In 2004, E and D were higher in *L. lepidus* colonies and lower in the other sites compared to 1992.

Species hierarchies—The order of species abundances in similar habitats was compared between years. Uncommon species (<0.02% cover) were removed, leaving 50 species in the analysis (1992 = 43 species; 2004 = 50 species). When species occurred only once, the comparison was excluded. Ranks changed substantially between years in each habitat type (Table 7). Spearman's rank correlations (S_r) within types between years were low: pumice, $S_r = 0.388$, $P < 0.05$; pyroclastic, $S_r = 0.382$, $P < 0.08$; drainage, $S_r = 0.718$, $P < 0.001$; *Lupinus*, $S_r = 0.554$, $P < 0.004$. We compared habitat types within years. S_r in 1992 ranged from 0.469 (drainage to *Lupinus*) to 0.822 (pyroclastic to *Lupinus*; mean = 0.673). In 2004, all rank correlations between habitats were larger except that of the *Lupinus* to pyroclastic comparison. S_r in 2004 ranged from 0.682–0.875 (mean = 0.791). These contrasts indicated that species are becoming more widely distributed, with less difference between habitats.

The low correlations between years indicated that relative species abundances changed greatly. *Agrostis scabra*, *Castilleja*, *Elymus*, *Polygonum*, and *Populus* became relatively more common, and mosses all became much more abundant. *Racomitrium* became dominant in many locations, and *Polytrichum* became an important subordinate. *Lupinus latifolius* expanded on pumice and pyroclastic habitats, but declined in drainages. Many of the initial colonists (pioneers) became proportionally less abundant (e.g., *Anaphalis*, *Chamerion*, *Eriogonum*, and *Luzula*). Only *Hypochaeris* generally retained its share and on pumice it increased, while *Saxifraga* declined on typical sites but increased in *Lupinus* colonies.

DISCUSSION

The landscape created by the 1980 eruption has developed rapidly since 1992 when vegetation was generally sparse. Dense vegetation was then confined to scattered wetlands, a few refugia on the eastern end of the study area (Fuller and del Moral, 2003), and *Lupinus* colonies. *Lupinus* and mosses have become widely distributed, and many other species have become common. Based on permanent plot data, much of the increase has occurred after 2000 (del Moral, 2004). As sites developed, *Lupinus* tended to promote other species through N-fixing, while other species have become sufficiently dense to inhibit development of other species. The balance between facilitation and inhibition appears to have altered, changing the rules for success (cf. Callaway and Walker, 1997).

Community types—While we described seven community types, each is variable, and none is closely correlated to habitats or to environmental variables. Plots assigned to different CTs overlap in DCA, and CTs show considerable variation. Vegetation could only be poorly predicted by CCA. The prin-

TABLE 7. Changes in the relative abundance of species. Values are the abundance ranks, stratified by habitat in 1992 and 2004, from which Spearman rank correlations were calculated.

Species	Pumice		Pyroclastic		Drainage		Lupine patch	
	1992	2004	1992	2004	1992	2004	1992	2004
Achillea millefolium	20	15	21	22	20	18	22	23
Agrostis pallens	6	7	5	16	13	8	9	5
Agrostis scabra	21	9	13	7	10	10	17	7
Alnus viridus	18	16	—	28	29	23	13	8
Anaphalis margaritacea	5	18	1	10	3	15	6	20
Carex mertensii	12	14	10	19	7	14	10	19
Castilleja miniata	26	8	—	6	—	9	20	9
Chamerion angustifolium	13	26	2	21	4	21	12	22
Cistanthe umbellata	15	19	19	9	14	17	21	24
Elymus elymoides	—	24	—	24	—	28	24	—
Epilobium spp.	24	21	15	20	25	24	—	15
Eriogonum pyrolifolium	11	31	16	29	19	31	26	—
Grimmia sp.	—	10	24	11	—	7	—	10
Hieracium albiflorum	17	12	8	8	11	11	14	11
Hypochaeris radicata	10	5	4	4	6	4	4	6
Juncus parviflora	16	17	14	15	8	13	19	13
Luetkea pectinata	17	29	18	27	18	27	15	16
Lupinus latifolius	9	4	—	14	5	12	2	—
Lupinus lepidus	1	1	3	2	2	2	1	1
Luzula parviflora	7	27	11	—	16	26	16	25
Penstemon cardwellii	2	6	6	13	12	6	5	12
Penstemon sericea	14	23	—	23	21	29	27	27
Phacelia hastata	23	28	22	28	22	20	25	26
Polygonum minimum	22	13	20	3	15	5	—	3
Polytrichum juniperinum	—	3	—	12	—	16	30	14
Populus balsamifera	—	22	—	17	—	19	31	21
Pseudotsuga menziesii	25	30	12	18	23	26	18	18
Racomitrium canescens	8	2	9	1	9	1	3	2
Salix commutata	3	11	7	5	1	3	7	4
Saxifraga ferruginea	4	20	17	26	17	22	23	17
Vaccinium membranaceum	27	25	—	—	27	30	11	28

cipal predictors of variation remain related to spatial landscape factors, not to local conditions. We conclude that stochastic factors related to dispersal and establishment still determine species composition on these young surfaces, and in most places deterministic factors related to competition and local soil conditions have not resulted in significant species turnover. Thus, while vegetation has become differentiated, community types remain loosely defined.

Species patterns—Species lacked the strong ties to environmental factors that typify more developed vegetation. The regression of species to CCA axes provided only moderate correlations. The best relationships were for species found at the extremes of one or both axes (e.g., *Lupinus latifolius*) and which were not widely distributed (e.g., *Saxifraga*). The distribution of most species was poorly explained, with $r^2 < 0.1$ with four predictors.

The lack of strong correlations implies that many species remain where they were first established when there were few competitors. They have persisted and expanded, even though they occupy suboptimal habitats. As the vegetation develops, it is likely that competitive interactions will limit many species to environments to which they are better adapted. As that process unfolds, we expect that analyses such as the CCA reported here will yield higher correlations.

Dominance hierarchies—The community types demonstrated strong differences in cover, diversity, and equitability.

Percentage cover was highest where mosses and *L. lepidus* dominated. Diversity and equitability were lowest when percentage cover was highest because only a few species produce the cover, leading to pronounced dominance.

Stronger dominance by a few species has led to lower diversity and dominance indices since 1992, except where *Lupinus* dominated. In *Lupinus* colonies, strong dominance, with little moss cover, produced very low diversity (H'), evenness (E), and dominance (D) values. These measures subsequently increased, reflecting less dominance by *Lupinus*. In the other habitat types, either dominance was reduced or it remained the same, even though the number of species increased. In pumice, pyroclastic, and drainage habitats, a few species became dominant. Often these dominants were mosses that were later colonists not pioneers. Thus, we observed the initial stages of the development of typical dominance hierarchies, also reflected in changing species ranks. Until dramatic changes in physical vegetation structure occur (e.g., through the invasion of conifers), existing species are likely to expand differentially so that dominance hierarchies will develop. Because these dominants will be those better adapted to a particular site, one result is that closer ties to the local environment should develop.

Implications—This study demonstrated large increases in vegetation cover on the Pumice Plain since 1992. Correlations between vegetation patterns and environmental and landscape factors remained weak, suggesting that heterogeneous patterns

of invasion and establishment have not yet been obliterated by deterministic factors such as competition or moisture gradients. Community types remained poorly differentiated and poorly correlated with environmental factors. They therefore fail to meet our criteria for true community types. Species composition of community types was variable. Both indirect (DCA) and direct (CCA) methods demonstrated large amounts of unexplained variation. Species displayed some correlations to environmental factors, but large residuals of unexplained variation remained for all species. Thus, the evidence for deterministic patterns also remains weak. We expect that unexplained variation of vegetation patterns in this landscape will decline with time, but that a large residual will remain (cf. Økland, 1999). Dispersal effects, priority effects, and stochastic processes are likely to persist. If a given species has a low probability of reaching identical sites, then links between distributions of species and their environment are weak (cf. Ozinga et al., 2005).

Once established, many species persist even when confronted by superior competitors (Tagawa, 1992; Eriksson and Eriksson, 1998). Continued occupancy of a site also alters soils. As a result, pioneers often dictate conditions for future colonization (Magnússon et al., 2001). Stochastic events that permit the development of heterogeneous vegetation may promote the eventual development of a mosaic representing alternative stable states in one habitat (Belyea and Lancaster, 1999; Petraitis and Latham, 1999; Savage et al., 2000). *Lupinus* colonies, in particular, create conditions where a few species respond to enhanced fertility (*Agrostis scabra*, *Hypochaeris*, and *Polytrichum*) and vegetation development is hastened. Less dense vegetation with little moss may be better suited to invasion by conifers, leading ultimately to woodland patches. All these changes have promoted more pronounced dominance hierarchies, suggesting that biological factors are becoming stronger. However, it is unlikely that vegetation mosaics will become homogeneous. Dominance varies in space and dominance patterns should persist. This result has implications for how communities assemble and for restoration.

The barren landscape on the north slope of Mount St. Helens continues to develop, but the process is far from complete. Vegetation continues to expand and develop while *Lupinus* continues to undergo regular massive population fluctuations at intervals of 5–6 years. In 2005, populations of *Lupinus* had collapsed everywhere on the Pumice Plain. Competitive hierarchies were more prominent than in 1992, suggesting that less stochastic, competitively based mechanisms are starting to become prominent. However, herbivores everywhere alter these vegetation patterns (Bishop et al., 2005) and can mediate vegetation mosaics. Future studies of the effects of dominant species (e.g., *Lupinus*, *Racomitrium*, *Agrostis*) on the invasion of species characteristic of more developed vegetation will provide insights into how later stages of primary succession develop. Our studies support a model in which priority and stochastic processes preclude close ties between species and environmental factors and foster heterogeneous vegetation. Predicting future vegetation is therefore problematic. However, we also show that spatial factors are crucial to community assembly, knowledge that can be applied directly to vegetation management.

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AMERICAN JOURNAL OF BOTANY [Vol. 92

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