Early primary succession on Mount St. Helens, Washington, USA

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Abstract. The north slope of Mount St. Helens was sampled with 141 circular 100-m^2 plots to describe vegetation and environmental patterns 13 yr after the 1980 eruption. At least 114 vascular plant taxa were encountered. We recognized four habitat types: Refugia, Pumice barrens, Pyroclastic surfaces and Drainages. A fifth category, Lupine patches, includes samples on primary surfaces that were rapidly colonized. Refugia provided small enclaves where underground portions of several species survived the eruption. They retained an inconsistent array of forest understory species and contained 86 species (mean = 20.8 per plot). Refugia are dominated by woody species such as *Penstemon cardwellii*, *Rubus* spp., *Ribes* spp. and *Alnus sinuata*, with herbs such as *Agrostis diegoensis*, *Luzula parviflora* and *Anaphalis margaritacea*. *Anaphalis* represents a suite of species that invaded Refugia after the eruption. Diversity (N_2 and H') is significantly greater in Refugia than in any other habitat. No plants survived on primary sites, which remain sparsely vegetated and dominated by readily dispersed taxa. Total richness ranges from 36 species (9.9 per plot) on pyroclastic surfaces, through 42 species (11.2 per plot) in drainages, to 66 (11.7 per plot) on Pumice barrens. H' and N_2 of the three habitats do not differ significantly. Lupine-dominated vegetation occurs sporadically in Pyroclastic and drainage habitats. Lupine patches are characterized by high *Lupinus* cover and a suite of invaders. These sites have high cover and 52 species (12.6 per plot). H' and N_2 scores were significantly lower than any other habitat due to strong lupine dominance. Canonical Correspondence Analysis showed that site history and slope contributed most to species composition. Geographic effects accounted for 10 - 25 % of the explained species-environment relationship. Forest understory species have migrated only short distances and have made negligible contributions to vegetation development. A few species common in Refugia, including *Agrostis diegoensis* and *Carex mertensii*, have invaded barren surfaces, but most have not. Refugia also have been invaded by open site species abundant on the Pumice Plain. The heterogeneity of plots within habitat types and small statistical linkage of vegetation to environmental and spatial factors suggests that stochastic events have played a leading role in early primary succession.

Keywords: Canonical Correspondence Analysis; Detrended Correspondence Analysis; Primary succession; Stochastic process; Volcano.

Introduction

The unusual lateral eruption of Mount St. Helens, Washington, on 18 May 1980, devastated a huge area and created many new habitats. The Pumice Plain, a 20 km^2 area on the north side of the volcano, bore the brunt of the eruption. On this plain, new substrates resulted from an avalanche, a massive lateral explosion, pyroclastic flows and mudflows. Tephra of variable texture subsequently covered these habitats to varied depths. Primary successional processes and recovery patterns on the Pumice Plain were described by Wood & del Moral (1988), del Moral & Wood (1988), del Moral (1993) and del Moral & Wood (1993 a, b). This study describes vegetation on the Pumice Plain 13 yr after the eruption. Most sites are colonized by immigrants, but survivors from Refugia in gullies or on steep north-facing slopes augment colonization of nearby primary sites.

Community composition in early successional communities can be influenced by random events such as dispersal, invasion and weather (Talling 1951; Margalef 1963). Indeed, stochastic processes may determine vegetation patterns over large scales (Collins et al. 1993; Collins & Glenn 1990, 1991). Del Moral et al. (mscr.) determined that species composition within nearly identical depression features on the Pumice Plain was variable and unrelated to environmental factors. The scale of this study is much larger, with samples from several habitat types. Do harsh conditions and limited colonization prevent a marked correlation between species composition and environmental factors (cf. Chesson & Case 1986; Davey & Rothery 1993), or do site history and habitat type strongly influence early species composition?

Here we assess the relationships between vegetation and physiographic and geographic factors. Our focus is the role stochastic factors may play in the establishment of vegetation.

Material and Methods

Study area

The Pumice Plain was formed on the north slope of Mount St. Helens (46° 12' N, 122° 11' W). The western Plain was formed by a debris avalanche and by subsequent pyroclastic flows. Portions of this site were further impacted by lahars spawned until 1984. Most drainages continue to be eroded, thus arresting succession. The eastern Plain was scorched by the lateral blast and seared by subsequent pyroclastic flows. Coarse pumice fell during the first and several subsequent eruptions. 13 years of erosion have dissected the landscape, forming drainages flowing from the crater. Pumice has decomposed to a fine texture, wind has removed fine surface materials and water has carved channels to reveal pre-eruption surfaces in some places.

Del Moral & Bliss (1993) summarized climate and substrate conditions of the Pumice Plain. Precipitation occurs primarily as snow from October to May. During summer, rainfall is episodic and variable. Established plants rarely experience drought, but seedlings may die on rapidly drying surfaces (Chapin & Bliss 1988). Nutrients, particularly nitrogen and phosphorus, are scarce (del Moral 1993; del Moral & Wood 1993a).

Four habitat types occupy the Pumice Plain. Pumice barrens occur where the previously existing vegetation was eliminated by the blast or pyroclastic flows and covered by deep air-fall pumice deposits. These barrens are concentrated on the eastern half of the Pumice Plain. Pyroclastic sites have surfaces that were ejected at very high temperatures and are relatively free from large-scale erosion. Mudflows swept down broad drainage courses through pumice and over pyroclastic sites. These surfaces remain unstable and were heavily altered by erosion. Materials in drainages may have originated with the 1980 eruption or may be composed of materials formed during previous eruptions. Refugia include those habitats on which some original vegetation survived. Most Refugia occur on north-facing slopes east of the debris avalanche. Here, the force of the blast was ameliorated to varying degrees. Some soil, seeds, buried plant organs or, possibly, stems survived. No conifers survived and relict vegetation is usually dominated by forest understory shrubs and herbs, with contributions from immigrants from surrounding barrens.

Scattered on pyroclastic and stable drainage surfaces are special sites that developed dense *Lupinus lepidus* colonies within the first two years after the eruption. These patches are a singular biotic feature of the Pumice Plain. They create biological oases that have facilitated invasions of other species (Wood & Morris 1990; del Moral 1993; del Moral & Wood 1993a) and

represent a special case of primary succession. The origin of these populations remains unknown, but genetic evidence (J. Bishop pers. comm.) implies that all *L. lepidus* on pyroclastic surfaces are derived from a few invaders. Sites dominated by *L. latifolius* were included with *L. lepidus* patches for these analyses.

Sampling

We sampled 141 circular 100-m² plots in 1992 to reflect the range of upland vegetation and environments. Vegetation data were percentage cover of each species in each plot, determined to the nearest 0.01 m² for species with under 5 % cover using a grided quadrat frame. Thereafter, cover was estimated visually to the nearest 1 % up to 20 % and in 5 % increments thereafter. Elevation was recorded in 10 increments (low to high); percent slope was converted to a 5-state scale (level to steep) and aspect was converted to an exposure scale of 1 = protected, north to 7 = south, exposed, after Whittaker (1960). The location of each plot was recorded on a grid with 168 units with 14 rows (west to east, X) and 12 columns (north to south, Y) on a map of the Pumice Plain. These nominal variables characterized habitat types: refugia, pumice barrens, drainages and mudflows, and pyroclastic surfaces. Lupine patch, a vegetation category, was considered a distinct habitat type since the presence of lupines significantly modifies barrens and pyroclastic surfaces.

A comparison of selected Refugia with adjacent barren plots and more distant barren plots was made. We selected 13 Refugia and matched them with 12 Barren plots within 20 m (Near) and with 12 barren plots over 100 m away (Far). One Refugium was matched with only a Near plot, a second with only a Far plot. If Refugia have a significant impact on the rate or direction of succession, then Near plots should have more species and greater cover than Far plots.

Data analysis

Detrended Correspondence Analysis (DCA) was used to obtain indirect ordinations (Hill 1979). DCA produces axes on which one unit is about one half-change in species composition (Hill & Gauch 1980). 10 plots that included both primary and Refugia surfaces were excluded. The remaining 131 plots were analyzed with DCA to determine overall patterns before more detailed studies were conducted. Species with fewer than three occurrences were deleted, leaving 75 species in the analysis. Cover percentages were log-transformed and remaining infrequent species were down-weighted.

Canonical Correspondence Analysis (CCA, ter Braak 1986; 1987; 1988a, b) is a direct ordination method that

relates environmental variables to vegetation and species patterns. Palmer (1993) provided a clear explanation of the method and demonstrated that it is robust and usually preferable to DCA. CCA calculates the effectiveness of the ordination, expressed by the proportion of the variation explained on each of the first four axes; the correlation between each canonical axis and each species axis and an estimate of the species variation explained by the measured variables. The correlation of each variable to canonical axes provides insight into factors that may control vegetation structure. Monte Carlo permutation tests of the first CCA and of the trace were performed to determine if the observed patterns differed from a random relationship (ter Braak 1990).

The full data set was analyzed with CCA after excluding the 10 heterogeneous plots with both relict species and primary elements. Species with less than three occurrences were deleted, rare species were downweighted; cover values were log-transformed. Detrending did not improve the analysis. Elevation and *Y*-position scores were highly correlated since the Pumice Plain slopes gradually downward from south to north. Therefore, *Y* was deleted from the general analysis.

Geographic position plays an important role in determining which species colonize a site (del Moral & Bliss 1993). Legendre & Fortin (1989), Leduc et al. (1992) and Borcard et al. (1992) outline how CCA can separate environmental from spatial variation. The species data were analyzed as follows: (a) constrained by the environment, (b) constrained by spatial factors, (c) constrained by environment after spatial effects are removed and (d) constrained by spatial factors after removing environmental effects. *X* and *Y* coordinates were used in this analysis.

Results

Floristics

Species frequencies differed among the habitat types and most of the 114 species did not exceed 10 % frequency in any habitat (App. 1). There is a well-defined set of species nearly restricted to Refugia, including forest shrubs and herbs, but lacking conifers. Common species include *Aruncus sylvester*, *Carex rossii*, *Ribes bracteosum*, *Rubus spectabilis* and *Vaccinium membranaceum*. Other typical montane forest understory species are sporadic and are also confined to Refugia. These species include *Amelanchier alnifolia*, *Clintonia uniflora*, *Lilium columbianum*, *Sambucus racemosa*, *Sorbus sitchensis*, *Spiraea densiflora*, *Tiarella trifoliata*, *Trillium ovatum* and *Veratrum viride*. These species rarely occur on primary surfaces.

Some common relict species have colonized the Pumice barrens. Ongoing permanent plot studies on the Pumice Plain demonstrate that these species were absent or rare prior to 1986 but have expanded greatly since then (Wood & del Moral 1988; del Moral & Bliss 1993). These species include *Agrostis diegoensis*, *Carex limnophila*, *C. mertensii*, *Luetkea pectinata*, *Lupinus latifolius*, *Luzula parviflora*, *Penstemon cardwellii* and *Saxifraga ferruginea*. Several of these have become locally abundant, suggesting the importance of Refugia to colonization dynamics.

Several species are common on all substrates. Based on their rarity in undisturbed habitats on Mount St. Helens (del Moral & Wood 1993a), these species appear to have invaded Refugia since 1980. These species include *Anaphalis margaritacea*, *Epilobium angustifolium*, *Hieracium albiflorum*, *Hypochaeris radicata* and *Salix barclayi*, each of which has excellent dispersal powers (Wood & del Moral 1987).

Most species confined to barren habitats are good dispersers with broad distributions, but most are infrequent (App. 1). These species include exotics, annuals, species uncommon in forested environments, or wetland plants. Species include *Carex phaeocephala*, *Epilobium paniculatum*, *Equisetum arvense*, *Eriogonum pyrolifolium*, *Festuca arundinacea*, *Juncus bolanderi*, *Poa incurva*, *Senecio sylvaticus*, *Spraguea umbellata* and *Trifolium repens*. Only *Eriogonum* and *Spraguea* are common in native, well-developed subalpine meadows.

General community structure

The cover and rank order of species common in at least one habitat or community type are listed in App. 2. The species are listed in rank order by mean cover in Refugia, which included many species found in other habitats in addition to narrowly restricted species. Total mean cover of each type is shown at the bottom.

Several features emerge from App. 2. Relict vegetation is heterogeneous. Even *Penstemon cardwellii*, the most common species, has mean cover of 3.97 %. Total cover among these plots varied from 2 % to over 100 %. Lupine patch cover is always high and dominance is pronounced. *Hypochaeris radicata* is the only exotic species that attains significant cover.

The barren habitat types are floristically similar and have low cover. *Agrostis diegoensis*, *Anaphalis margaritacea*, *Epilobium angustifolium*, *Hypochaeris radicata*, *Lupinus lepidus* and *Salix barclayi* are typically among the leading dominants in all barren sites.

Spearman rank correlation values (Siegel 1992) were calculated among the habitats using species cover rank (App. 2) to determine the degree of structural similarity. An *r*-value of 0.446 is needed for a comparison to

show a statistically similar structure ($P < 0.01$). Refugia vegetation is independent of pumice ($r = 0.442$) and of Drainage plots ($r = 0.375$) and only moderately correlated to Pyroclastic plots ($r = 0.589$) and Lupine patches ($r = 0.577$). Refugia have several common woody species absent elsewhere plus many forest species otherwise rare. Lupine patches are correlated to the other primary surface habitats, despite much higher cover. Rank correlations with drainages ($r = 0.810$) and pyroclastic surfaces ($r = 0.834$) are high. Many of the samples of these habitats are close to Lupine patches and draw from a similar pool of immigrants. The correlation of Lupine patches to pumice surfaces ($r = 0.650$) is lower, possibly an effect of the distance separating these plots.

Drainages and Pyroclastic surfaces are generally in the same locations and draw from a similar pool of invaders. They are strongly correlated ($r = 0.768$). The correlation of drainages ($r = 0.597$) and Pyroclastic sites ($r = 0.591$) to pumice are similar. The distance from pumice plots to most other primary surfaces may explain these reduced correlations.

We characterized each plot by cover, Shannon-Wiener diversity (H') and the inverse of Simpson's dominance index (N_2, Krebs 1989). App. 2 gives mean cover of the more common species in each habitat type. The three primary surfaces have mean species richness ranging from 9.9 species on Pyroclastic sites to 11.7 species per 100 m^2 on Pumice barrens (Table 1). Lupine patches have richness comparable to barren sites (12.6 per plot). Refugia have 20.8 species per plot, a value significantly greater than that of all other sites. Mean H' of Refugia is significantly greater than all other sites, a combination of high richness and limited dominance. H' of the Lupine patches is 0.84, a value very significantly lower than all other habitats. The H's of Pumice, Drainages and Pyroclastic habitats are not statistically different from each other and are intermediate to Refugia and Lupine patches.

N_2 reveals further structure details. N_2 of the Refugia is 5.13, significantly greater than the three barren habitats (Table 1). Refugia are diverse and few species recur often. Refugia are fragments of heterogeneous understory vegetation augmented by invasions of species adapted to open conditions. N_2 of Lupine patches is significantly lower than all other habitats. Primary sites are dominated by *Anaphalis margaritacea* or *Carex mertensii*, often with few other common species. Therefore, dominance is intermediate between Lupine and Refugia.

Effect of distance

The positive effects of relict vegetation on the rate of community development has been emphasized by several workers (cf. Franklin et al. 1985). We compared the species composition of Near and Far plots with nearby Refugia to determine if there was any such effect.

Mean richness of Far plots (10.2 species) is significantly less ($P < 0.0002$) than Near plots (16.5 species) and less ($P < 0.0001$) than Refugia (21.7 species). Near plots have significantly fewer species ($P < 0.05$) than Refugia. Mean H' of Far plots is 1.685, significantly lower than both Near plots ($H' = 2.625$, $P < 0.002$) and Refugia ($H' = 2.887$, $P < 0.001$). Refugia and Near plots do not differ significantly in H'.

There is also a trend for N_2. That of Refugia is 6.21, which is not significantly greater than that of Near plots ($N_2 = 4.60$, $P < 0.15$), but significantly greater than Far plots ($N_2 = 2.26$, $P < 0.001$). N_2 of near plots is significantly greater than that of Far plots ($P < 0.01$).

An inspection of the species composition of the 37 plots in this comparison shows that Near plots have several species typical of the nearby Refugia, but Far plots do not. Refuge species common on Near plots include *Achillea millefolium, Aquilegia formosa, Carex rossii, Juncus mertensianus, Lupinus latifolius, Luzula parviflora, Ribes bracteosum, Rubus parviflorus* and *Sedum oreganum*. In most cases, these species are uncommon on Near plots and it is premature to speculate on whether these invaders from Refugia will accelerate succession. The contribution of late seral species from Refugia to barren sites is geographically and quantitatively limited at present. As physical amelioration continues on the barren sites, this situation may change dramatically.

Table 1. Structural measures of the five habitat types. Within a column, values sharing the same superscript are not significantly different ($p < 0.05$) by a simple *t*-test. S.D. = Standard deviation.

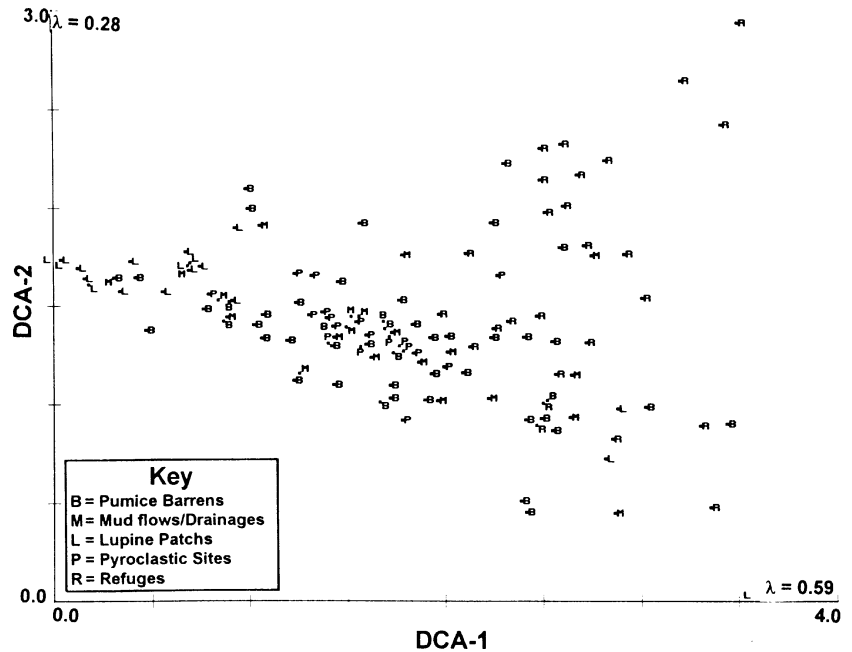| Habitat	N	Mean richness	S.D.	H'	S.D.	N$_2$	S.D.
Relicts	27	20.8 [a]	6.9	2.83 [a]	0.75	5.13 [a]	2.53
Pumice Barrens	49	11.7 [b]	4.0	2.11 [b]	0.69	3.57 [b]	1.35
Drainages/Mud flows	20	11.2 [b]	3.9	2.37 [b]	0.77	3.75 [b]	1.96
Pyroclastic Flows	17	9.9 [b]	2.9	2.06 [b]	0.47	3.25 [b]	1.11
Lupine Patches	18	12.6 [b]	7.2	0.84 [c]	0.75	1.59 [c]	1.57

Fig. 1. Detrended Correspondence Analysis of all sample plots: distribution of plots in the diagram of axes 1 and 2.

Detrended Correspondence Analysis

The first two axes account for 15.8 and 7.4 % of the variance, respectively. The DCA 1 is over 3.5 half-changes long. These are typical values when there are so many species. Total variance (inertia) is 3.738.

The five habitat types are only moderately well sorted in the ordination space. Refugia have high scores on both axes (Fig. 1). A few Lupine patch plots that are dominated by *L. latifolius* and associated with lush herbs and low, woody vegetation are in Refugia. They have high DCA-1 scores and relatively low DCA-2 scores. Typical Lupine patch plots are dominated by *L. lepidus* and associated with species common to barren sites. These plots have low DCA-1 scores. Pumice barren, Pyroclastic and Drainage plots are scattered throughout the diagram, with no clear pattern to their distribution.

Detailed conclusions about species patterns on the Pumice Plain are difficult to draw. Species with large positive scores on both axes occur in Refugia. These species include shrubs such as *Ribes* spp., *Rubus spectabilis* and *Vaccinium membranaceum* and herbs such as *Athyrium distentifolium*, *Disporum hookeri*, *Smilacina racemosa* and *Trillium ovatum*. Species with low DCA-1 scores, but high DCA-2 scores occur in mesic or moist sites, usually along drainages. These species include *Agrostis exarata*, *Equisetum arvense*, *Epilobium watsonii* and *Potentilla glandulosa*. Species with low DCA-1 and low DCA-2 scores are from open, mesic sites. *Lupinus lepidus*, *Hypochaeris radicata*, *Carex spectabilis* and *Spraguea umbellata* are typical of

this group. Species with low DCA 2 scores are uncommon, found in more stable, often moist habitats. These species include *Agrostis scabra*, *Carex mertensii*, *C. limnophila*, *Epilobium angustifolium*, *Luetkea pectinata*, *Lupinus latifolius* and *Saxifraga ferruginea*. The remaining species are widely dispersed and show no particular preference. *Anaphalis margaritacea* is nearly ubiquitous and occurs in the center of the diagram. *Agrostis diegoensis* is more closely associated with Refugia and *Hieracium albiflorum* with more mesic sites.

DCA yields little insight into the factors controlling vegetation, but it emphasizes that Refugia and Lupine plots are distinct and that the primary surfaces are floristically similar. We did not analyze these axes further by indirect means since we used direct gradient analysis.

Canonical Correspondence Analysis

Complete data set

Total variance (inertia) is 3.738. The first CCA eigenvalue is four times larger than the second and accounts for most of the explicable variation. CCA 1 accounts for 12.0 % of the species data variation and 51.6 % of the species-environment relationship. The species- environment correlation for this axis is moderate (0.891). The canonical eigenvalues account for only 23.3 % of the total variance, but Monte Carlo permutations showed that both CCA 1 and the overall trace were significant ($P < 0.01$).
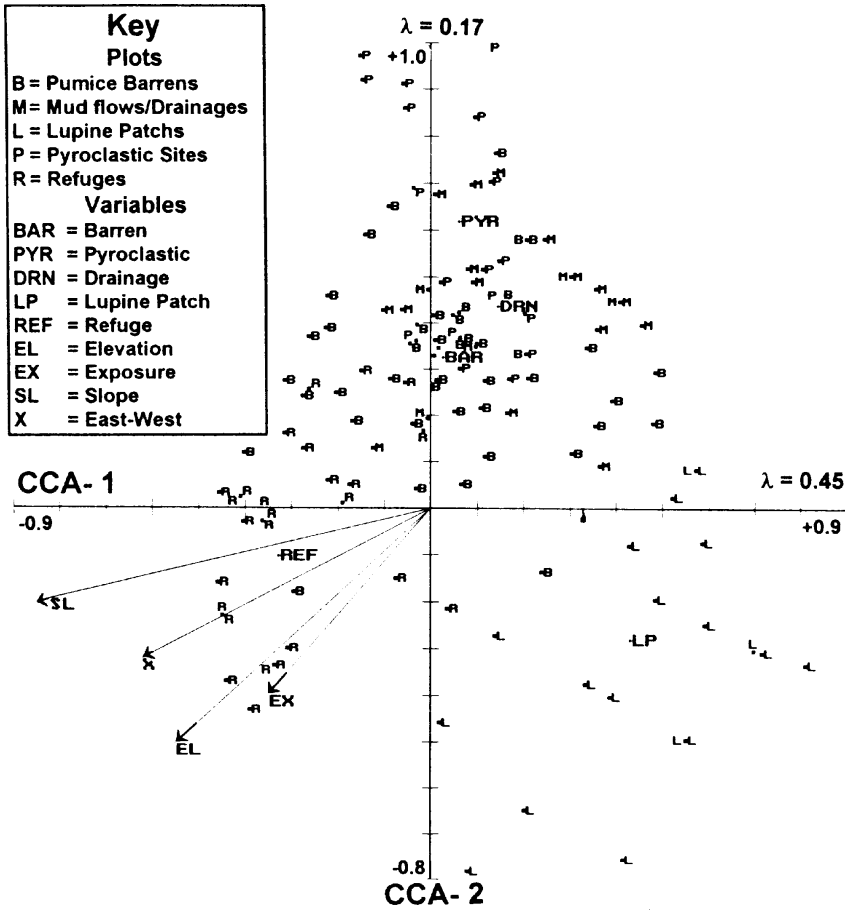
Fig. 2a. Canonical Correspondence Analysis: biplot of all samples in the diagram of axes 1 and 2.
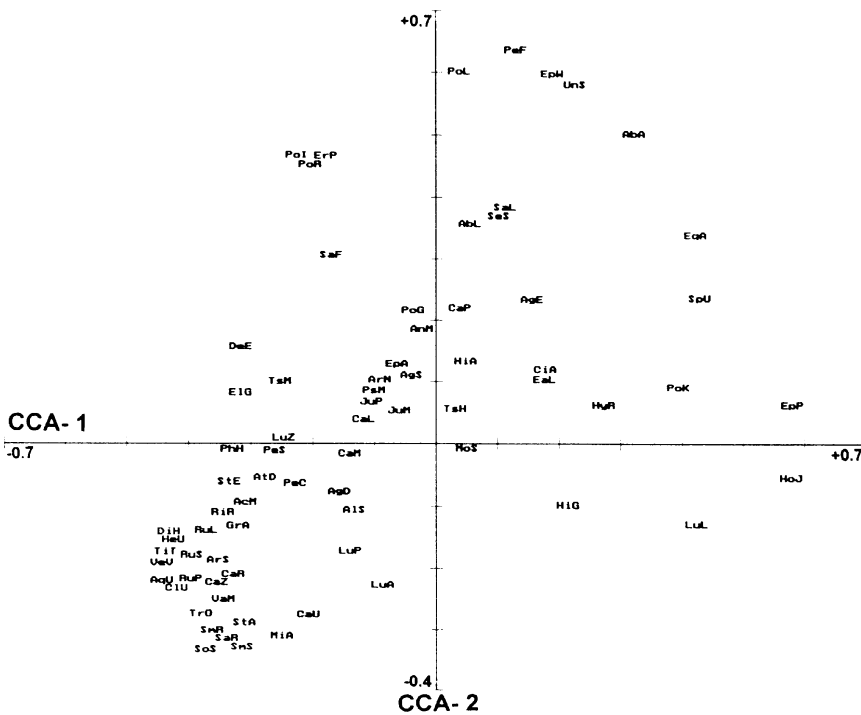

Fig. 2b. Canonical Correspondence Analysis of all sample plots: distribution of species. For species codes, see App. 1.

Table 2 summarizes the inter-set correlations of environmental variables with the first two canonical axes. The best predictors of species composition were slope and if a plot is either a Refuge or a Lupine patch. CCA 2 has weak relationships to elevation and barren habitats.

Bi-plots summarize the relationship between environmental variables and plots. Vectors lead to the centroid of meristic variables. Nominal variables are not drawn as vectors, but as centroids. Plot positions are linear combinations of the environmental variables and species scores are the weighted means of the sample scores.

Fig. 2a is the bi-plot of environmental factors with plot distributions and Fig. 2b is the scattergram of the species. Refugia (R) have negative to very low positive scores on both CCA axes. Pyroclastic plots (P) have CCA 1 scores near zero, but all have high CCA 2 scores. Drainage plots (D) are distinct, with high CCA 1 scores and moderate positive CCA 2 scores. Pumice plots (B) are centered in the middle of CCA 1 with a low, positive CCA 2 score. This habitat type is spread over a wide portion of the graph. Lupine patch plots (L) have positive CCA 1 scores and negative CCA 2 scores. CCA 1 is strongly influenced by the dichotomy between Lupine patches (LP) and relict (REF) vegetation. The t-value for relicts is -7.64, indicating its significance. Pumice (BAR), pyroclastic (PYR) and drainage (DRN) variables cluster closely. Slope (SL) is also very important ($t = -5.88$), because steep slopes also tend to be Refugia. However, steep slopes are also more mesic than others since they invariably face north. The separation between Pumice and Pyroclastic plots is also related to position (X, $t = -7.12$) since Pumice plots are concentrated on the east side of the Pumice Plain and Pyroclastic plots are more westerly. CCA 2 is poorly defined, accounting for 19.6 % of the species-environment correlation. Elevation (EL) is most strongly corre-

lated with this axis ($t = -6.58$), while each nominal variable is also significant.

The clearest species patterns that emerge are the number of species associated with Refugia and that *Lupinus lepidus* (LuL) is aligned with Lupine patches (Fig. 2b). Common species are centrally located. The dominant species in Refugia include *Carex rossii* (CaR), *Ribes bracteosum* (RiB), *Rubus lasiococcus* (RuL), *R. spectabilis* (RuS), *Sorbus sitchensis* (SoS) and *Vaccinium membranaceum* (VaM). These species are common in late seral communities (Klinka et al. 1989), but were also common in the pre-eruption montane forest understories of the Mount St. Helens area (Kruckeberg 1987; del Moral & Wood 1988b). These species have not spread significantly onto the barren areas, though some samples occur a few meters from Refugia.

Lupinus lepidus is the only common species that is isolated in the Lupine patch portion of Fig. 2b. The remaining species are common in barren habitats and occur as later invaders of Lupine patches. These include *Anaphalis margaritacea* (AnM), *Epilobium* spp. (EaA and EaL) and *Hypochaeris radicata* (HyR).

This analysis suggests that the presence of a biological legacy is the most important factor explaining these patterns. Refugia are clearly identified in this analysis. The chance establishment of lupines on barren plots is the second most important factor. Other primary surfaces have different histories, but similar species composition, which suggests the importance of dispersal. Elevation and X explain a small portion of this variation.

Table 2. Inter-set correlations of environmental variables with canonical axes: All plots; Relict and Lupine Patch plots; and Primary Surface plots (Pumice, Pyroclastic and Drainages). Scores are $\times 1000$. Most important values are in bold.

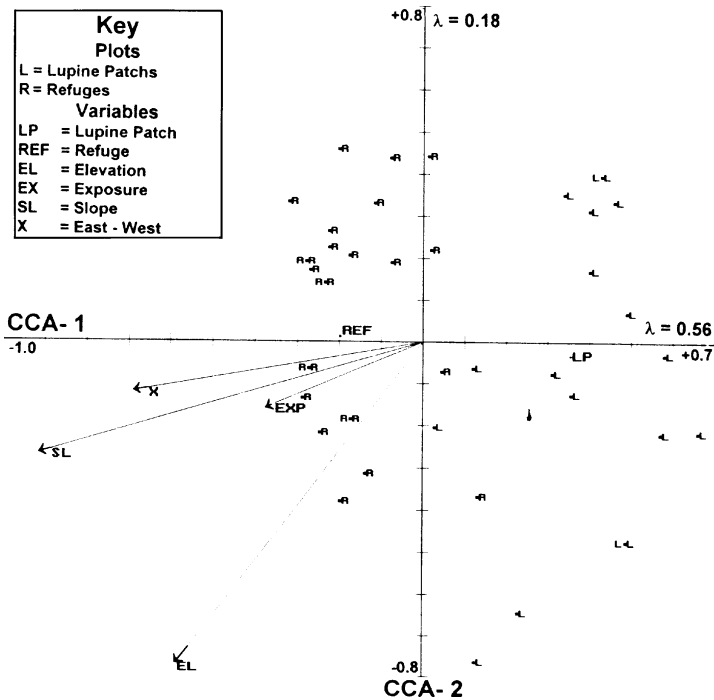| Variable	All		Refugia/Lupine		Primary	
	Axis 1	Axis 2	Axis I	Axis II	Axis I	Axis II
Species/Canonical Correlation	**891**	**764**	**935**	**852**	**729**	**657**
Elevation - EL	− 493	**− 386**	− 542	**− 619**	**435**	**396**
Slope - SL	**− 735**	− 148	**− 829**	− 240	322	− 19
Exposure - EX	− 314	− 304	− 338	− 210	91	**508**
East/West - X	− 557	− 247	**− 603**	− 115	**478**	185
Refugia - REF	**− 692**	− 185	**− 819**	5	-	-
Pumice - PUM	32	**334**	-	-	133	60
Pyroclastic - PYR	37	**− 338**	-	-	− 33	− 11
Drainage - DRN	87	227	-	-	− 132	-64
Lupine Patch - LP	**667**	**− 375**	**849**	− 64	-	-

Fig. 3. Canonical Correspondence Analysis of Refugia and Lupine patch plots: bi-plot in the diagram of axes 1 and 2.

High-cover plots

The data were divided into high-cover plots composed of Refugia and lupine-dominated sites and low-cover plots consisting of barrens, Drainage and Pyroclastic sites.

The CCA of high-cover sites included 45 plots with 72 species that occurred more than twice. The first two axes account for 18.2 % and 5.7 % of the variance, respectively. Table 2 summarizes the species-environment interactions in high-cover plots. CCA axis 1 is correlated with the first species CCA ($r = 0.935$) and accounts for 52.9 % of the species-environment relationship. CCA axis 2 is correlated to the second species CCA ($r = 0.853$) and accounts for 16.7 % of the species-environment relationship. The environmental data explain 34.4 % of the unconstrained variance. Both CCA-1 and the total trace are significant ($P < 0.01$; Monte Carlo permutations).

The principal factors governing high cover vegetation are slope (SL, $t = -4.37$) and location ($X, t = -4.72$). Despite the large correlations between CCA-1 and the nominal traits Refuge and Lupine patch, neither t-value was significant (Table 2). Slope is important because Refugia occur primarily on steep slopes, while Lupine patches occur on flats or gentle slopes. East-west position is important because Refugia occur mainly in the east, Lupine patches to the west. The second CCA explains little. Both types occur over a range of elevations.

There is a clear distinction between Refugia and Lupine plots (Fig. 3). Most species with large N_2 values are common in both habitats. Species with negative CCA-1 scores are predominantly relicts. Those with high positive scores are concentrated in Lupine patches or occur throughout the sample.

Because Refugia and Lupine patches have distinct histories and limited species overlap, each was analyzed independently. When Refugia were analyzed, the sum of the unconstrained eigenvalues is 2.234, while that of all canonical axes is 0.691 (30.9 %). Both the first CCA and the trace are significant Monte Carlo permutation). Elevation (and Y) accounts for most of the first CCA variation, while exposure accounts for most of the second CCA variation.

In the Lupine patch analysis, the sum of unconstrained eigenvalues was 1.746, while that of the canonical axes was 0.927 (53.1 %). CCA 1 is related to slope and Y-scores. The *L. latifolius* plots occur on steeper, north-facing slopes, while the *L. lepidus* plots occur on gentle slopes. The second CCA is related to elevation and to exposure. Both the first CCA and the overall trace are significant ($P < 0.01$ by Monte Carlo permutation). A greater degree of explained variance occurs with Lupine patches for two reasons. First, there is a well-defined floristic dichotomy between relict *L. latifolius* plots and primary *L. lepidus* plots. Second, Lupine patch plots are more homogeneous than relict plots. Environmentally similar Refugia may be floristically distinct (see App. 2 to compare frequencies).
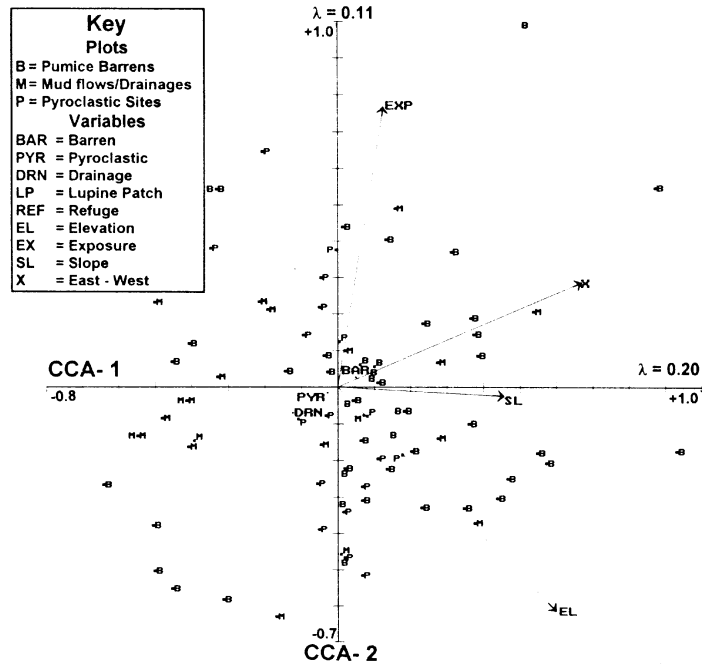
Fig. 4. Canonical Correspondence Analysis of Pumice barrens, Mud flows and Drainages, and Pyroclastic plots: bi-plot in the diagram of axes 1 and 2.

Low-cover plots

Canonical Correspondence Analysis of 86 barren plots was pursued as described in the Methods after excluding species with fewer than three occurrences. The first two species axes account for only 5.7 and 3.2 % of the variance, suggesting a diffuse data set. The species-environment correlations are weak ($r = 0.720$ for CCA axis 1, $r = 0.654$ for CCA-2.) CCA-1 accounts for 40.8 % of the species-environment relationship, CCA-2 for 22.6 %. Together, all canonical eigenvalues account for 14.1 % of the unconstrained eigenvalues.

Though weak, CCA-1 is significant ($P < 0.01$, Monte Carlo permutation.) East-west position (X, $t = 5.06$) and elevation (EL, $t = 4.65$) are the leading factors, though each is weak (Table 2). There is a floristic difference both from west to east and with elevation. The three barren habitats have low correlations with all axes and none is significant. CCA-2 relates primarily to exposure (EX, $t = 4.93$), which affects moisture and elevation (EL, $t = -4.07$).

Fig. 4 reveals that the floristics of these three habitat types overlap broadly. The nominal variables BAR, DRN and PYR occur near the origin of the plot. There is a weak tendency for Pumice barrens plots (B) to dominate extreme values. The elevation gradient is related to moisture, while the X dimension is related to the geographic position of survivors.

Only eight species had N_2 scores more than 10 (*Agrostis diegoensis, Anaphalis margaritacea, Carex mertensii, Epilobium angustifolium, Hieracium albiflo-*

rum, Hypochaeris radicata, Lupinus lepidus and *Penstemon cardwellii*). Most of these species are seral species, characteristic of disturbed sites. Lowland *Hypochaeris* is an aggressive exotic species (Hitchcock & Cronquist 1973; Turkington & Aarssen 1983). Species are well distributed in this canonical space, but there are no strong patterns. Extreme species are rare and occur in plots adjacent to Refugia (e.g. *Ribes lacustre, Smilacina stellata*). There is a cluster of species from moist habitats with negative CCA-1 scores and slightly positive CCA-2 scores. These species include *Alnus sinuata, Agrostis exarata, Equisetum arvense, Epilobium watsonii* and *Polystichum lonchitis*. Other patterns are difficult to discern. High elevation plots have more sedges, lower elevation plots have more grasses. Eastern plots are more likely to have species such as *Achillea millefolium, Eriogonum pyrolifolium* and *Luzula parviflora* than are western plots. This may reflect somewhat less stressful conditions in those plots that received less direct impacts.

Spatial analysis

Spatial analysis enables a partition between environmental, environment plus spatial and spatial components of explained variation, plus undetermined components (Borcard et al. 1992). We obtained no useful insights from including quadratic and cubic derivatives of the spatial coordinates, so they were not included in this analysis. We used the same set of environmental

data (including habitat types) and the same options as for the complete data set described above, but included the *Y*-dimension. Total explained variance is 23.3 %. Unexplained variance, which includes stochastic events and sampling effects, accounts for 76.7 %. Environment alone explained 17.4 %, spatial explained 2.5 % and environment plus spatial effects combined explained 3.2 %. Very little of the explained variance is due to geographic location alone.

Discussion

This study presents a static view of a dynamic landscape. Other studies on Mount St. Helens demonstrated that vegetation is changing rapidly in some places, slowly in others (Halpern et al. 1990; del Moral & Bliss 1993). One purpose of this study was to assess the degree to which existing vegetation can be explained on the basis of crude measures of site quality and by position measures.

All sites sampled for this study are successional and will change over the coming decades. Relict vegetation includes a diverse assemblage drawn from different microsites, with little in common. Cover varied widely and no species had more than a mean cover of 4 %. Species essentially confined to Refugia rarely occurred in more than half of the Refugia sampled. Refugia include a range of initial conditions, differential survival and different subsequent invasions by non-forest species. The result is a set of vegetation samples including both early pioneer and forest understory species to various degrees.

Relict vegetation contributed few species to barrens beyond a few meters, and barren site vegetation structure was altered only in close proximity to the relicts. Refugia vegetation now consists of surviving forest understory species and of many species that have invaded from barren sites. Relict species have had little impact on the Pumice Plain. However, since many of these species have recovered reproductive abilities, their presence assures rapid colonization of barren sites once physical and biological amelioration permit their survival. Species of the forest margins and moist subalpine meadows have invaded broadly across the Pumice Plain. These species are not the first plants in a particular habitat, but they are often the first to occupy a particular microsite. They are becoming increasingly common. Relatively few plants of these species are derived directly from Refugia. Most are second- and subsequent-generation individuals produced on barren sites or which have invaded from outside the blast zone.

The ways in which the initial lupine colonists arrived by 1981 to found dense patches on Pyroclastic surfaces remains unclear (see del Moral & Bliss 1993). Pioneer lupines became established in scattered locations and altered the rate of biotic facilitation by shading, carbon accumulation and nitrogen fixation (Halvorson et al. 1992) and greatly improved the survival chances of subsequent colonists (Morris & Wood 1989; del Moral & Wood 1993a). Lupine patches dominated by *L. lepidus* are homogeneous, having formed in a relatively small area and receiving immigrants from the same limited pool. Refugia dominated by *L. latifolius* are less homogeneous, but contrast sharply with other Refugia and with *L. lepidus* patches.

Statistically, relict vegetation and Lupine patches are the best explained by CCA, primarily because of the sharp contrast between these two types of high cover plots. Refugia are quite variable, yet 30.9 % of the species variation is explicable. Lupine patches are homogeneous and occur in two distinctive types of habitats, thus more than 53 % of the species variation is explicable. The presence of *Lupinus* spp. ameliorates the physical environment and creates an intensely competitive environment. Lupines therefore have formed the strongest links with other species, resulting in the most predictable set of plots.

Barren sites, consisting of Pumice, Pyroclastic surfaces and Drainage courses, are structurally and floristically similar. The correlation between floristic axes and canonical axes is weak and this data set is the least well explained. This suggests that dispersal events override differences in disturbance history, at least in the early stages. The presence or absence of mycorrhizae on the Pumice Plain explains little of the observed variation (J. H. Titus, mscr.). Elevation and east-west position, both of which affect the seed rain, are the most important factors.

Refugia have a legacy of forest understory species and have accumulated vagile species. Lupine patches formed fortuitously and have accumulated a quantitatively distinct flora. The other primary surfaces are more similar to each other, but each has distinguishing features that vary in space. As these systems develop, they may become more predictable as biotic interactions restrict species to narrower distributions and strengthen the relationships between environmental factors and species occurrence. Vegetation on this landscape is more closely coupled to the environment where recovery has proceeded most quickly. In addition to Refugia and Lupine patches, new wetlands have developed quickly. Moisture levels strongly condition vegetation on the Pumice Plain (Titus & Stanford mscr.).

However, factors that control vegetation patterns on the Pumice Plain remain localized and are strongly affected by chance and landscape features rather than by predictable relationships to the physical environment

(see Lavorel & Lebreton 1989). Lupine patches themselves appear to have originated as a result of a few dispersal events. Position on the landscape with reference to Refugia affects species composition of barren sites only slightly, but more than do elevation, slope or aspect. Invasion of the Pumice Plain does not occur along fronts from intact vegetation or island Refugia. Rather, invasion proceeds from isolated individuals whose progeny colonize locally (Moody & Mack 1988). These nascent populations expand, then coalesce (del Moral & Wood 1993b).

Many different species can establish in the same microsite type (del Moral 1993). This suggests that species composition is largely a result of lottery-style invasion (Sale 1977). Sufficient time has not elapsed to detect any significant turnover, but it is possible that a carousel mechanism, where different species successively occupy the same microsite, will occur (see Hanski 1982; Collins et al. 1993; Kikvidze 1993; van der Maarel & Sykes 1993). As yet we have no evidence that early pioneers other than lupines can exclude other early pioneers from their vicinity.

Historical events can decouple plant-environment interactions for many years (Gauch 1983) and affect community structure indefinitely (Gleason 1939; McCune & Allen 1985). Multiple succession paths or novel plant communities may result (Tagawa 1992). After 13 seasons, the Pumice Plain is sparsely and unevenly occupied. Some structure is apparent, but many seemingly similar sites differ radically in their composition.

We conclude that early reassembly of plant communities on the Pumice Plain is controlled primarily by stochastic events such as Lupine patch formation and low probability dispersal. Unpredictable historical events, such as the season of the eruption and the persistence of relict vegetation, play an important, though secondary, role. Geographic effects such as dispersal distance are the main determinants of barren site structure. Environmental factors as yet play a limited role in governing community structure. We predict that the combined effects of landscape effects and stochastic processes will continue to strongly influence community structure for many decades. Such processes must contribute to the consistently large unexplained variance in most vegetation studies.

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App. 1. Species encountered and their frequency in each habitat type.

Species name	Code	Growth form[1]	Status[2]	Refugia	Lupine patch	Barren	Pyroclastic	Drainage
Abies amabilis[3]	AbA	CT	N	.037		.018		
A. lasiocarpa	AbL	CT	N	.079		.055	.118	
Achillea millefolium	AcC	RP	N	.222	.211	.055	.059	.136
Actaea rubra	AcR	TP	N	.037				
Agrostis diegoensis	AgD	RP	N	.704	.684	.618	.294	.409
A. exarata	AgE	FP	N	.111	.263	.055		.091
A. scabra	AgS	FP	N	.148	.421	.200	.294	.091
Alnus sinuata	AlS	TS	N	.333	.158	.036		.045
Amelanchier alnifolia	AmA	TS	N	.074				
Anaphalis margaritacea	AnM	RP	N	.963	.842	.909	1.00	1.00
Aquilegia formosa	AqF	TP	N	.111		.018		
Arnica cordifolia	ArC	RP	N	.148	.105		.059	
Aruncus sylvester	ArS	TP	N	.407	.052	.018		
Aster ledophyllus	AsL	FP	N	.074				
Athyrium distentifolium	AtD	RP	N	.296	.105	.073		
Blechnum spicant	BlS	RP	N		.105			
Campanula scouleri	CaS	RP	N	.036			.059	
Carex limnophila	CaL	FP	N	.667	.316	.145		.227
C. mertensii	CaM	RP	N	1.00	.526	.782	.765	.636
C. pachystachya	CaP	FP	N	.185	.052	.236		.136
C. phaeocephala	CaX	FP	N			.018		
C. praticola	CaT	FP	N		.105	.028		
C. rossii	CaR	FP	N	.444		.055		.045
C. spectabilis	CaS	RP	N	.074	.158			.045
Carex sp.[3]	CaU	—	—	.111	.105	.018		
Castilleja miniata	CaZ	FP	N	.037	.052			
Cirsium arvense[3]	CiA	RP	E	.111	.263	.091		.318
Clintonia uniflora	ClU	RP	N	.148				
Deschampsia atropurpurea	DeA	FP	N	.037				
D. elongata	DeE	FP	N	.037		.018	.059	
Disporum hookeri	DiH	RP	N	.074			.059	
D. smithii	DiS	RP	N	.074				
Elymus glaucus	ElG	FP	N	.148		.036	.059	.045
Epilobium alpinum	Eal	RP	N	.074	.316	.145	.118	.091
E. angustifolium	EpA	RP	N	.963	.684	.818	1.00	.909
E. paniculatum	EpP	AN	N		.158	.018		
E. watsonii	EpW	FP	N		.052	.036		
Equisetum arvense	EqA	RP	E		.052	.036		
Eriogonum pyrolifolium	ErP	TP	N		.052	.073	.059	.091
Festuca arundinacea	FeA	RP	E		.052	.018		
Fragaria virginiana	FrV	RP	N	.037	.052			
Gaultheria ovalifolium	GaO	DS	N	.037		.014		
Gnaphalium uligonosum	GnU	AN	E	.037	.052	.091		
Heuchera micrantha	HeU	TP	N	.074		.036		
Hieracium albiflorum	HiA	FP	N	.704	.684	.691	.882	.864
H. gracile	HiG	FP	N	.074	.105		.118	
Hordeum jubatum	HoJ	FP	N		.158		.	
Hypochaeris radicata	HyR	F-TR	E	.778	.737	.836	1.00	1.00
Juncus bolanderi	JuB	RP	N		.052			
J. bufonius	JuO	AN	N	.018				
J. mertensianus	JuM	RP	N	.444	.211	.164		.045
J. parryi	JuP	FP	N	.593	.579	.345	.235	.227
Lactuca muralis	LaM	AN	E	.037		.018		
Lomatium martendalei	LoM	TP	N	.037				
Luetkea pectinata	LuP	DS	N	.296	.211	.309	.059	.091
Lupinus latifolius	LuT	TP	N	.593	.263	.091		.227
L. lepidus	LuL	TP	N	.259	.842	.600	.529	.636
Lilium columbianum	LiC	BP	N	.037				
Luzula parviflora	LuP	RP	N	.963	.263	.164	.118	.227
Microseris alpestris[3]	MiA	TP	N	.074	.105			
Mimulus lewisii	MiL	RP	N	.111				
Montia parviflora	MoP	FP	N	.073		.091		
M. siberica	MoP	AN	N	037				
Penstemon cardwellii	PeC	DS	N	.963	.526	.545	.529	.545
P. serrulatus	PeS	DS	N	.074	.158	.055		.045
Petasites frigidus	PeF	RP	N	.037	.091			
Phacelia hastata	PhH	TP	N	.185		.036	.059	.045
Poa gracillima	PoG	FP	N	.018				
P. incurva	PoI	FP	N	.018				
Polygonum kellogii	PoK	AN	N	.074		.036	.059	.227
Polystichum lonchitis	PoL	RP	N	.148	.052	.073	.176	.045
Populus balsaminifera	PoP	DT	N		.052			
Potentilla glandulosa	PoG	FP	N	.185		.091	.118	.182
Pseudotsuga menziesii	PsM	CT	N	.370	.158	.109	.235	.091
Ribes bracteosum	RiB	MS	N	.481				
R. lacustre	RiL	MS	N	.148		.018		
Rubus parviflorus	RuP	DS	N	.185		.018		
R. lasiococcus	RuL	DS	N	.296				
R. spectabilis	RuS	MS	N	.519	.059	.091		
Rumex acetosella	RuA	FP	E	.037				
Salix barclayi	SaB	MS	N	.519	.421	.491	.647	.455
Sambucus racemosa	SaR	TS	N	.111				
Saxifraga ferruginea	SaF	FP	N	.370	.211	.218	.059	.273
Sedum oregana	SeO	RP	N	.018				
Senecio sylvaticus	SeS	AN	E	.055	.176	.091		
Smilacina racemosa	SmR	RP	N	.185		.018		
S. stellata	SmS	RP	N	.074		.036		
Sonchus asper	SoA	AN	N	.018				
Sorbus sitchensis	SoS	TS	N	.148				
Spergularia diandra	SpD	AN	E	.059	.045			
Spiranthes romanzofiana	SpR	TP	N	.037				
Spiraea densiflora	SpD	MS	N	.037				
Spraguea umbellata	SpU	FP	N		.052	.200	.235	.364
Stellaria sp.	StE	FP	E?		.052	.018		
Streptopus amplexifolius	StA	RP	N	.148				
Tellima grandiflora	TeG	RP	N	.074				
Tiarella trifoliata	TiT	RP	N	.111				
Trifolium repens	TrR	RP	E		.052			
Trillium ovatum	TrO	BP	N	.222				
Tsuga heterophylla	TsH	CT	N	.037	.052	.018	.059	.045
T. mertensiana	TsM	CT	N	.111		.018		
Vaccinium membranaceum	VaM	MS	N	.630	.105			
V. parviflorum	VaP	MS	N	.037				
Valeriana sitchensis	VaS	FP	N	.037				
Veratrum viride	VeV	RP	N	.074				
Unknown Grasses[3]	UnG	RP	N	.037			.018	.059
Mosses	MoS	—	N	.815	.632	.400	.529	.564
Liverwort	LiV	—	N	.037		.018		
Total number of species	—	—	—	86	52	66	36	42

[1]Categories: CT = Coniferous Tree; DT = Deciduous Tree; TS = Tall Shrub; MS = Medium Shrub; DS = Dwarf Shrub; RP = Rhizomatous perennial (including stolons); TP = Tap-rooted perennial; BP = Bulbous perennial; FP = Fibrous-rooted perennial; AN = Annual/biennial.

[2]Status: N = Native; E = Exotic.

[3]These taxa may include these related species. *Abies procera, Agoseris aurantiaca, Arnica latifolia, A. nevadensis, Carex paysonis, Cirsium vulgare,* and *Festuca occidentalis* have been identified on the Pumice Plain uplands.

App. 2. Mean cover (%) of common species[1] in each major habitat type, listed in order of rank in Refugia. Values are $\times$ 100. Samples deleted from Canonical Correspondence Analysis are not included.

Species	Refuge	Pumice		Drainage		Pyroclastic		Lupines	
	$n = 25$	Rank	$n = 49$	Rank	$n = 21$	Rank	$n = 17$	Rank	$n = 19$
Penstemon cardwellii	397	4	27	10	4	7	11	4	113
Anaphalis margaritacea	269	2	62	3	44	1	108	5	71
Agrostis diegoensis	191	5	26	11	4	5	16	8	17
Luzula parviflora	160	6	25	14	1	11	2	11	8
Carex mertensiana	136	10	15	7	7	10	7	9	17
Vaccinium membranaceum	132		—	—	—	—			
Alnus sinuata	118	21	< 1	15	< 1	—	7	21	
Rubus spectabilis	110	—	16	< 1	13	< 1	—		
Ribes bracteosum	108	—	—	—	—				
Rubus lasiococcus	104	—	—	—	—				
Lupinus latifolius	97	8	21	5	9	14	< 1	2	790
Aruncus sylvester	89	—	—	—	—				
Epilobium angustifolium	78	11	10	4	10	2	64	6	25
Sorbus sitchensis	71	—	—	—	—				
Carex sp.	40	—	—	—	21	< 1			
Hypochaeris radicata	38	9	18	6	8	4	18	3	685
Carex limnophila	27	18	2	12	2	15	< 1	13	7
Juncus parryi	26	12	6	8	7	16	< 1	16	3
Rubus parviflorus	26		—	—	—	—			
Achillea millefolium	23	19	2	17	< 1	17	<1	19	1
Lupinus lepidus	23	1	64	2	56	3	22	1	4638
Clintonia uniflora	21	—	—	—	—				
Luetkea pectinata	18	15	5	18	< 1	18	<1	15	4
Pseudotsuga menziesii	16	22	< 1	19	< 1	12	2	14	7
Hieracium albiflorum	14	16	3	9	5	8	9	10	12
Agrostis scabra	12	20	2	—	19	< 1	12	9	
Salix barclayi	11	3	34	1	79	6	12	6	51
Saxifraga ferruginea	11	7	23	21	< 1	21	< 1	20	1
Castilleja miniata	8	—	—	—	22	<1			
Phacelia hastata	8	—	—	—	—				
Juncus mertensiana	6	17	3	20	< 1	20	< 1	17	2
Spraguea umbellatum	—	13	6	13	2	22	< 1	18	2
Eriogonum pyrolifolium	—	14	6	—	—	23	< 1		
Mean cover	32.52		4.50		2.60		2.88		70.56
Standard deviation	32.7		5.61		3.72		3.37		27.8

[1]Species with less than five occurrences are omitted unless they are locally abundant.