Primary succession trajectories on pumice at Mount St. Helens, Washington

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Abstract

Questions: Does vegetation become less variable over time? Do floristic trajectories converge during succession? Can either allogenic (external) or autogenic (internal) factors predict species patterns during succession?

Location: Pumice Plain of Mount St. Helens (46.23449°N; 122.15929°W, 1230 m a.s.l.), which was sterilized in 1980 by a direct volcanic blast, then buried in pumice.

Methods: We monitored a grid of 200 100-m^2 contiguous plots annually (1989–2010) and classified the 2010 data into five community types (CTs). We characterized plots using external (e.g. distance from relict sites) and internal (e.g. moisture) factors and clustered plots by position and habitat factors to assess trajectories. We used redundancy analysis (RDA) to assess relationships between vegetation and these variables over time. Mantel tests, similarity changes and detrended correspondence analysis (DCA) were used to evaluate successional trends.

Results: Five CTs were weakly related to habitats at this scale. Over time, vegetation became more homogeneous and successional trajectories of plots clustered by position and habitat factors became more similar or developed in parallel. The succession rate slowed fitfully as persistent species became dominant, while *Lupinus* fluctuated. Mantel tests indicated that relationships between species and environment were maximized using only autogenic factors. RDA found that autogenic factors were stronger than allogenic ones, while explained variance did not increase after 1992 and factor correlations to species stabilized by 1996.

Conclusions: The strength of links between vegetation and environment were weak at this scale, yet explained variation stabilized early in succession. As substantial vegetative variation persisted and convergence was far from complete due to weak links to habitat factors, habitat variation and stochastic establishment should be considered by vegetation managers.

Introduction

Traditional succession theory states that predictable autogenic (internal) factors determine the course of succession (i.e. trajectories; Toft & Elliott-Fisk 2002). However, autogenic factors may not produce predictable results (Walker & del Moral 2003). Instead, alternative trajectories can occur due to allogenic (external) factors that affect dispersal (Jones & del Moral 2005), as well as stochastic factors (Marteinsdottir et al. 2010). Control by autogenic factors (e.g. fertility) normally increases over time, especially when intensified by biotic effects (del Moral & Eckert 2005), but allogenic effects (e.g. distance to potential colonists) may persist. Thus, compositional variation should decline as the intensity of interactions increases, the vagaries of dispersal decline and microsite effects become muted (Suess & Schabe 2010). The degree to which heterogeneous vegetation may converge can be due to habitat heterogeneity (Kim & Yu 2009) or priority effects (Hejcmanova et al. 2010). Priority effects result if colonists inhibit the typical successional progress, leading to a vegetation mosaic poorly linked to predictive factors.

Links between species and autogenic factors may weaken when more specialized species become dominant (Carlson et al. 2010), so that the predictability of trajectories may not improve after early competitive sorting (Erfanzadeh et al. 2010).

Trajectories that lead to alternative communities are possible if biotic interactions are weak. While trajectories on environmentally similar sites normally converge (e.g. Bossuyt et al. 2005), contrasting sites can follow parallel or divergent trajectories (Lepš & Rejmánek 1991) in response to habitat variation and landscape effects (del Moral et al. 2010).

The new landscape on Mount St. Helens, developing since 1980, is an ideal place to study primary succession and to reveal mechanisms that shape community assembly. By the mid-2000s, desolate plains had become *Lupinus*-dominated meadows (Figure S1a, b; del Moral & Rozzell 2005). Vegetation assembly accelerated after 15 yrs (del Moral & Jones 2002), but may have slowed more recently (del Moral 2009). Early studies on Mount St. Helens showed that landscape effects explained vegetation patterns more effectively than did autogenic factors (del Moral et al. 1995), but more recent studies suggested that autogenic effects explain most variation relatively early in succession (e.g. del Moral 2009). However, no study on Mount St. Helens has demonstrated strong predictive relationships between explanatory factors and vegetation. Immature vegetation, residual stochastic effects and our inability to measure significant factors restrict predictability.

Understanding vegetation assembly allows for better landscape management (Densmore 2005) and conservation (Gondard et al. 2006). For example, allowing heterogeneous vegetation to develop can produce vegetation with greater resilience that can provide enhanced ecosystem services. To further this understanding, we ask: has the vegetation become more homogeneous as autogenic factors become increasingly dominant; does the rate of succession slow, as measured by species turnover; have explanatory factors become more predictive; and has the vegetation of this compact study area converged to similar composition?

Methods

Study site

The Pumice Plain study area is 4.5 km NE of the lava dome of Mount St. Helens (46.23449°N, 122.15929°W, 1212–1244 m a.s.l.). An intense lateral blast and subsequent pumice deposits from eruptions that started on 18.05.1980 (Swanson & Major 2005) destroyed all vegetation except in a few gullies. The grid features significant topographic variation and plots experiencing both primary and secondary succession from surviving vegetation. While we cannot extrapolate these local patterns to the entire landscape, they do suggest processes operating at a large scale.

Vegetation sampling

Permanent plots reduce errors inherent to chronosequence studies (Johnson & Miyanishi 2008). A grid of 200 contiguous 100-m^2 plots in a 10-column (east to west) by 20-row (north to south) array was established in 1989 to assess species expansion and the development of community structure. Plots were established to monitor initial colonization and the origin of secondary colonists, making a contiguous array mandatory (del Moral & Jones 2002).

We estimated species cover with the following index system: 1 = less than six individuals (0.1%), 2 = six to 20 individuals (0.2%), 3 = >20 individuals; or cover of 0.25–0.5 m^2 (0.375%), 4 = >0.5–1 m^2 (0.75%), 5 = >1–2 m^2 (1.5%), 6 = >2–4 m^2 (3.0%) and 7 = >4–8 m^2 (6%). Values >8 m^2 per plot were recorded without conversion to an index score. R.d.M. determined cover from the vertical projection of the canopy of each species annually. For descriptive purposes, we transformed the indices to the percentage cover shown in parentheses.

Explanatory variables

Explanatory variables include allogenic factors external to the grid and autogenic factors associated with a plot (Table 1). We calculated relative solar radiation from slope, aspect and latitude (McCune & Keon 2002). Visible light (lux) was determined with a light meter parallel to the surface at the top of the vegetation around solar noon on 20 Jul 2010. We collected soil samples from near each plot centre. Soil moisture was determined gravimetrically from samples taken 2–5 cm below the surface. Soil pH was determined in the laboratory from a 1:1 soil:water paste. Soil texture was determined by sieving samples into gravel (>5 mm), sand (2–5 mm), silt (250 μm to 2 mm) and fines (<250 μm). Elevation was determined from a digital map.

These variables had multistate descriptors: geographic position (20 rows and ten columns) correlated to latitude and longitude, respectively; topography (smooth, recent gully or old gully); state of residual soil (lacking, recently exposed or long-exposed relict sites); distance from surviving vegetation (surviving relicts, adjacent, 10–20 m distant or >20 m); and exposure to wind (protected, moderately protected or exposed to the prevailing wind). Relict sites harboured surviving plants, although in 1989 vegetation remained poorly developed and confined to deep gullies (see del Moral & Eckert 2005). We deleted silt to avoid autocorrelation. Elevation (quantitative) and row position (categorical) were correlated ($r > 0.85$), so row

Table 1. Allogenic and autogenic explanatory variables used in redundancy analyses.

Variable	Comments
Allogenic factors	
Elevation (m)	From electronic topographic map (correlated to latitude)
Distance from relicts	Four categories (0 = relict; 3 > 20 m)
Easting	Longitude (column position, 10 categories)
Northing	Latitude (row position, 20 categories)
Autogenic factors	
Solar radiation	Relative, calculated from slope, aspect and latitude
Visible light (lux)	Determined using a light meter parallel to surface
Soil moisture (%)	Gravimetric, wet weight determined in field
Soil pH	1:1 soil:water paste determined in lab
Soil texture categories	Gravel, sand, silt and clay, determined by sieving
Exposure to wind	Local topography and aspect relative to prevailing wind (three categories)
Topography	Smooth, recent gully or relict gully
Residual soil	None, recently exposed or long-exposed relict

position was deleted. Elevation is a position variable because its range is small and has little effect on temperature differences. We therefore treat it as an allogenic factor. (trial analyses using 'Row' rather than 'Elevation' produced similar results.)

Analyses

We calculated plot species richness, cover index and Shannon diversity (H′= [-Σ $p_i$logp_i], where p_i is the proportion of the cover index of the ith species; PC-ORD, version 5.0, MjM Software Design, Gleneden Beach, OR, US).

We classified 2010 plot data into community types (CTs) using agglomerative flexible sorting ($\beta = -0.25$) with Euclidean distance of the index values (PC-ORD, version 5.0). We similarly classified each plot into habitat types (HTs) using autogenic factors. We used χ^2 tests to compare classifications based on species with those based on habitat.

We used Mantel tests to compare matrices of Euclidean distances of plots in species space with those of plots in explanatory variable space (PC-ORD, version 5.0). Mantel tests provide a t-value and the Mantel statistic (r). We estimated annual floristic changes for each CT using detrended

correspondence analysis (DCA; PC-ORD, version 5.0). Homogeneity within each CT was determined annually from the standard deviation (SD) of DCA scores in a group and by the percentage similarity among plots of a group. Eight groups of 16 contiguous plots were formed (SG). We excluded relict sites. Each cluster was separated from the others by at least 10 m. Within-group variation was assessed by standard deviation (SD) of the scores of the members of the group. For both spatial and habitat types in a year, we determined Euclidean distance in two dimensional DCA space between two groups and by the percentage similarity of each pair. Trends were assessed using linear regression.

Species composition of the 200 plots in each year was sufficiently similar that we could use linear redundancy analysis (CANOCO version 4.5, DLO-Agricultural Mathematics Group, Wageningen, NL) to explore relationships between species patterns and explanatory variables (Lepš & Šmilauer 2003). Cover values were regressed on explanatory variables to create fitted species score, and then we used principal components analysis to form canonical plot scores. We assessed variation by comparing the result to a null model (9999 permutations). The regression coefficient of each variable with each RDA axis estimated how well each variable predicted plot position, determined by a t-value ($df = 200$ samples – 12 variables – 1 = 187). Unexplained variation suggested the effects of unmeasured variables, sampling error and random processes. We applied covariance analyses for each year to partition explained variation into that associated with autogenic and allogenic factors.

We conducted descriptive analyses with Statistix 9 (Analytical Software 2008, Analytical Software, Tallahassee, FL, US). Comparisons within a year used one-way ANOVA (e.g. cover index scores of species in the CTs). We used repeat measures ANOVA for comparisons between years. ANOVAs were followed by Bonferroni difference tests. Parametric analyses of contiguous plots may create statistical problems. We divided the grid using a checkerboard system and compared structural parameters of CTs of each group. Results were similar, so for the descriptive purposes of this study, we report results for the full grid.

Results

Vegetation development

Vegetation on the Pumice Plain developed in three phases. From 1980 to 1995, species interactions were limited as richness accumulated. Cover and diversity increased slowly. From 1995 to 2003, while cover increases continued, richness stabilized and dominance hierarchies developed. *Lupinus lepidus* then endured several remarkable population fluctuations that resulted from herbivory

(Apple et al. 2009) and pathogens, its short life span and abnormal weather. During periods of lower *Lupinus* abundance, dominance by mosses and grasses increased, apparently in response to facilitative effects of *Lupinus*.

Clustering revealed five community types (CTs): four relatively similar types on primary surfaces and an outlier found in relict sites. Species composition, expressed as percentage cover, richness, total vegetation cover and diversity describe the vegetation (Table 2). The CTs demonstrated a distinct spatial pattern (Fig. 1a), clustering into significantly fewer spatially contiguous groups than in five trials that randomly assigned a CT to a position.

CT-A, with high cover and low diversity, was dominated by *L. lepidus* (Figure S2a) and mosses (*Polytrichum* and *Racomitrium*). CT-B was compositionally similar, but had less *Lupinus* and mosses and more *Penstemon* (Figure S2b); it had the least cover, the lowest mean richness and was common in exposed sites. CT-C occurred in more protected sites and differed from CT-A by lower *Lupinus* cover with more *Racomitrium*, *Penstemon* and *Agrostis*. CT-D was in protected sites and adjacent to relict plots (Figure S3); cover was low, but H′ was high; *Lupinus* and moss cover were low, while *Chamerion* was relatively abundant. CT-E, dominated by shrubs, was comprised of plots found in relict sites and more recently exposed soil. Since 1995, it has been structurally distinct, although dominance among several shrub species varied; *Salix* was common in these plots, while various tall shrubs formed locally dense thickets; *Luzula* and *Chamerion* were abundant and richness and diversity were the highest.

Table 2. Structure and species composition in five community types (CT). Values are mean percentage cover (derived by transformation from index scores); *N* = number of plots. Differences determined by ANOVA, followed by Bonferroni pair-wise comparisons. Superscripts indicate membership in homogeneous groups. Values in bold indicate >80% frequency in the CT. Species are in order of their DCA scores; CTs are in order of their mean DCA scores.

Species	CT-A (*n* = 43)	CT-B (*n* = 68)	CT-C (*n* = 44)	CT-D (*n* = 23)	CT-E (*n* = 22)	*P*<
Mean richness	16.3[bc]	15.1[c]	18.7[a]	17.7[ab]	20.3[a]	0.0001
Mean cover (%)	68.6[a]	25.9[c]	42.3[b]	21.6[c]	43.3[b]	0.0001
Mean index total	101.9[a]	57.5[c]	80.8[b]	62.3[c]	93.1[ab]	0.0001
Mean diversity (H′)	2.028[c]	2.404[b]	2.660[a]	2.714[a]	2.841[a]	0.0001
Lupinus lepidus	**45.5[a]**	**13.79[b]**	**10.0[bc]**	**2.92[d]**	**7.02[cd]**	0.0001
Polytrichum juniperinum	**9.70[a]**	**2.29[b]**	**9.93[a]**	**3.52[b]**	3.51[b]	0.0001
Racomitrium canescens	**4.80[b]**	**1.48[bc]**	**8.31[a]**	**1.39[c]**	1.20[c]	0.0001
*Juncus parryi**	**0.29**	**0.22**	**0.34**	**0.20**	**0.28**	0.0369
Penstemon cardwellii	**1.67[b]**	**2.31[ab]**	**3.31[a]**	**3.48[a]**	**2.51[ab]**	0.0178
Abies species*	0.39	0.05	0.08	0.07	0.89	0.0250
Carex pachystachya	0.24[b]	0.18[b]	**0.27[ab]**	0.20[b]	**0.31[a]**	0.0047
Pseudotsuga menziesii	0.21[b]	0.22[b]	0.96[a]	0.31[b]	0.29[ab]	0.0015
Agrostis pallens	**1.27[b]**	**1.55[b]**	**3.01[a]**	**2.73[ab]**	**3.30[b]**	0.0002
Poa incurva	0.16[ab]	0.002[ab]	0.07[a]	0.01[ab]	0.04[ab]	0.0112
Hieracium albiflorum	**0.16[bc]**	**0.13[c]**	**0.22[b]**	**0.20[bc]**	**0.38[a]**	0.0001
Carex mertensii	**0.4[b]**	**0.35[b]**	**0.43[b]**	**0.45[b]**	**1.16[a]**	0.0001
Salix sitchensis	**2.08[b]**	1.16[b]	**1.26[b]**	**1.58[b]**	**5.23[a]**	0.0001
*Luetkea pectinata**	0.61	0.53	0.52	0.68	**1.26**	0.0464
Anaphalis margaritacea	**0.26[b]**	0.19[b]	**0.31[b]**	0.54[ab]	**0.89[a]**	0.0001
Saxifraga ferruginea	0.08[c]	0.07[c]	0.18[bc]	0.48[ab]	0.70[a]	0.0001
Hypochaeris radicata	0.06[b]	0.04[b]	0.06[b]	0.15[b]	**0.61[a]**	0.0001
Luzula parviflora	0.08[b]	0.13[b]	0.45[b]	0.33[b]	**1.27[a]**	0.0001
Achillea millefolium	0.04[b]	0.05[b]	0.13[b]	0.02[b]	0.44[a]	0.0006
Castilleja miniata	0.31[b]	0.02[b]	0.28[b]	0.13[b]	**2.11[a]**	0.0001
Chamerion angustifolium	0.09[bc]	0.08[c]	0.19[bc]	0.64[b]	**1.51[a]**	0.0001
Vaccinium membranaceum	0.01[b]	0.02[b]	0.07[b]	0.03[b]	1.44[a]	0.0001
Carex spectabilis	0.00[b]	0.00[b]	0.00[b]	0.00[b]	1.15[a]	0.0001
Athyrium distentifolium	0.00[b]	0.06[b]	0.00[b]	0.08a[b]	0.45[a]	0.0034
Alnus viridus	0.00[b]	0.05[b]	0.08[b]	0.15[b]	1.15[a]	0.0080
Sambucus racemosa	0.00[b]	0.00[b]	0.00[b]	0.00[b]	0.25[a]	0.0024
Rubus lasiococcus	0.00[b]	0.00[b]	0.00[b]	0.00[b]	0.22[a]	0.0260
Rubus spectabilis	0.00[b]	0.00[b]	0.00[b]	0.03[b]	1.06[a]	0.0001
Ribes species	0.00[b]	0.00[b]	0.00[b]	0.00[b]	0.66[a]	0.0064

*Pattern of significant differences precluded use of homogenous group format.

Fig. 1. Distribution of (**a**) community types and (**b**) habitat types on the Pumice Plain grid, Jul 2010. Elevation generally increases from north to south.

We classified the plots into six habitat types (HTs) using autogenic factors. Those factors that differed across the types ($P < 0.05$; ANOVA) are shown (Table 3). HT-A occupied moderately exposed, gentle slopes with fine soil. HT-B was on more protected sites with coarse soil. HT-C was on higher, more exposed sites with finer textured soil. While HT-D was similar to HT-C, it occupied more protected habitats. HT-E contained exposed plots with substantial radiation and light; soil was relatively fine. HT-F included the relict sites; light and exposure were low because many of the plots were in gullies; soils were correspondingly coarse. The map of HT patterns shows that the habitats generally include several contiguous plots (Fig. 1b).

The relationship between the communities and habitats were evaluated with χ^2 and was modest ($\chi^2 = 96.5$ with 15 df). Most of the relationship was from CT-E that occurred predominantly in HT-F. This reflects the relationship between relict vegetation and a distinctive habitat. The other CTs were scattered among the remaining habitat types.

Vegetation structure dynamics

The vegetation has been relatively stable for several years, with the exception of pulses of *L. lepidus*. Prior to 2004, the vegetation had developed relatively smoothly from the blasted terrain despite highly variable summer weather and chronic disturbances from insects, pathogens and elk. We can visualize the dynamics of this vegetation using richness, cover index and H′ for each CT through time (Fig. 2a–c). In 1989, vegetation was sparse, even in what we later recognized as relict sites based on the presence of mature shrubs. Richness increased rapidly through 1995, then more slowly as dominance of *Lupinus* and mosses increased and ephemeral species were eliminated (repeated measures ANOVA; $P < 0.0001$). The cover index developed slowly, but significantly for each CT ($P < 0.0001$). Through 2001, the relict sites in CT-E had greater cover and structural variation than the others. After averaging *Lupinus* fluctuations, cover appeared to stabilize by 2007. Diversity (H′) increased until 1998, thereafter it declined as dominance hierarchies developed. Differences among the CTs in each year were significant. CT-E usually had the highest diversity, while CT-A developed the lowest diversity as mosses became abundant.

Species dynamics

Lupinus lepidus (Fig. 3a) increased progressively for a decade, then began a recurring pattern of rapid growth and precipitous crashes due to herbivory in 1999–2000, 2004–2005 and 2007–2008 (see Bishop 2002; J. G. Bishop, personal communication). These fluctuations affected most other species and augmented soil fertility (del Moral

Table 3. Mean value for significant environmental (autogenic) variables in six habitat types (HT). See Table 2 for description of statistics. See Table 1.

Variables	HT-A (n = 38)	HT-B (n = 20)	HT-C (n = 58)	HT-D (n = 21)	HT-E (n = 38)	HT-F (n = 25)	P <
Solar radiation*	1.078	1.040	1.037	1.076	1.083	1.029	0.0003
Visible light (lux)	742[b]	636[e]	683[d]	715[c]	783[a]	556[f]	0.0001
Exposure to wind	2.52[ab]	2.14[bc]	2.42[ab]	2.45[ab]	2.68[a]	1.88[c]	0.0001
Residual soil	1.11[b]	1.28[b]	1.21[b]	1.10[b]	1.13[b]	1.86[a]	0.0001
Gravel	0.159[b]	0.209[ab]	0.186[b]	0.170[b]	0.173[b]	0.239[a]	0.0005
Silt	0.495[a]	0.396[ab]	0.466[a]	0.462[a]	0.491[a]	0.365[b]	0.0001

*Pattern of significant differences precluded use of homogenous group format.
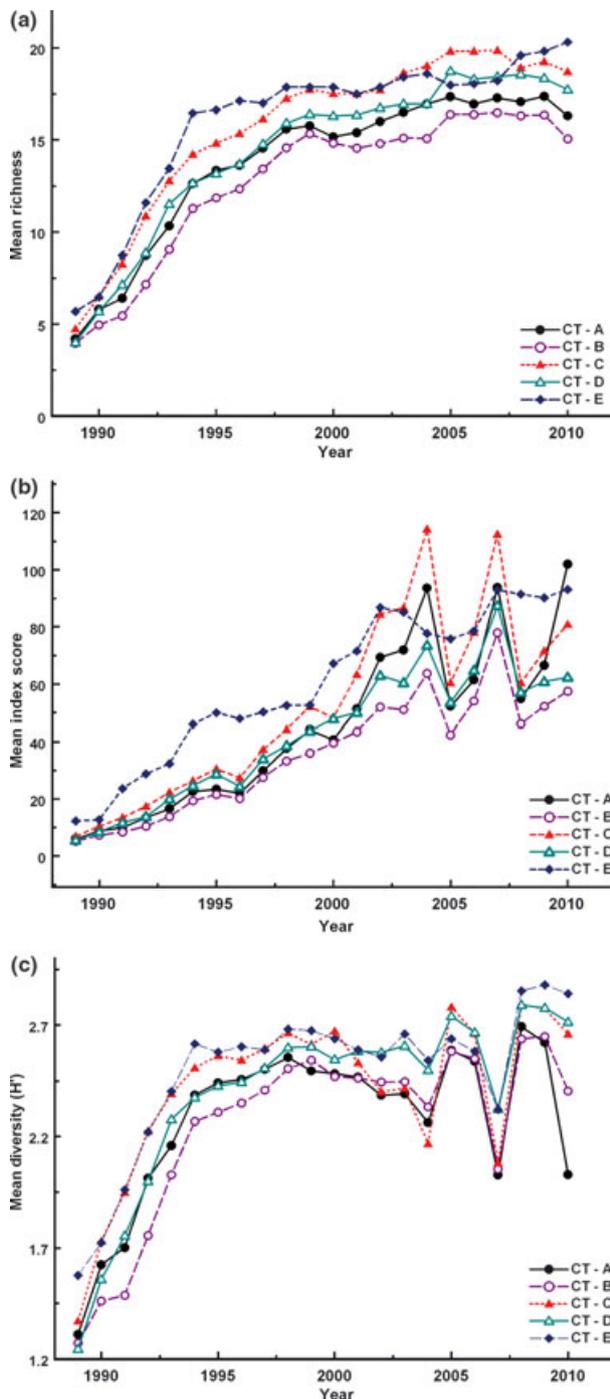
Fig. 2. Development of community structure on the Pumice Plain grid: (**a**) richness, (**b**) cover index and (**c**) Shannon diversity (H′).

& Rozzell 2005; Halvorson & Smith 2009). Common species (Fig. 3b) increased rapidly until 2001 then developed more slowly. Dense *Lupinus* during pulse years obscured moss cover, producing an artificial decline in these species. *Salix* appeared stable. Among less common species

(Fig. 3c), *Agrostis scabra* and *Anaphalis*, a pioneer species, declined after 2006, while *Luetkea* and *Juncus parryi* continued their persistent development. *Carex* species remained stable. Less common species (Fig. 3d) increased slightly or not at all. *Chamerion*, a pioneer, declined strongly except in relict sites. *Hieracium* and *Hypochaeris* (cf. Schoenfelder et al. 2010), the dominant pioneer species, increased until 2000, then stabilized. *Luzula* and *Juncus mertensianus* continued to increase. *Saxifraga* occupied disturbance-prone microsites and fluctuated widely.

Trajectory development

We explored vegetation trajectories using DCA. The mean position of each CT changed over time in two dimensions (Fig. 4; repeat measures ANOVA, $P < 0.0001$). The trajectory of CT-E developed over a shorter range than the CTs on primary surfaces. DCA-1 accounted for 21.1% of the variation ($\lambda = 0.323$), and DCA-2 for 6.7% ($\lambda = 0.103$). We estimated floristic distance (β diversity) traversed by each CT by comparing the mean scores in the first 3 yrs to the mean of the last 3. For DCA-1, CT-A shifted 1.45 half-changes (HC); CT-B shifted 1.41 HC; CT-C shifted 1.21 HC; CT-D shifted 1.11 HC; and CT-E shifted 0.96 HC. DCA-2 changes were even smaller for CT-A to CT-D (ca. 0.7 HC) and smaller for CT-E (0.46 HC). These temporal changes were significant over time in both axes. On DCA-1, the r^2 ranged from 0.767 (CT-C) to 0.902 (CT-E), but after 2005 changes were erratic. Non-linear regression [with (year × year) added], improved the fit. DCA-2 was little affected by *Lupinus*, and the linear regressions were significant; r^2 ranged from 0.877 (CT-E) to 0.954 (CT-D).

The rate of succession, measured by annual floristic change, declined. Linear regressions of the between-year differences (3-yr running average of Euclidean distances in three dimensions) in each primary surface declined after excluding the 1989–1990 comparison as follows: CT-A: $r^2 = 0.32$, $P < 0.007$: CT-B: $r^2 = 0.64, P < 0.0001$; CT-C: 0.508, $P < 0.0004$; CT-D: $r^2 = 0.726$, $P < 0.0001$. Annual changes in CT-E were not significant.

Trajectory convergence

DCA scores show how each CT trajectory developed relative to the others. The four primary-surface CTs are similar in composition and appeared to change in unison, while the relict CT-E seemed to diverge. Each CT became less variable over time as measured by linear regressions of the SD of DCA scores, even though fluctuating *Lupinus* abundance reduced the strength of these relationships. Reduced variation of DCA scores was also observed in each spatial group and in each HT (Table 4).
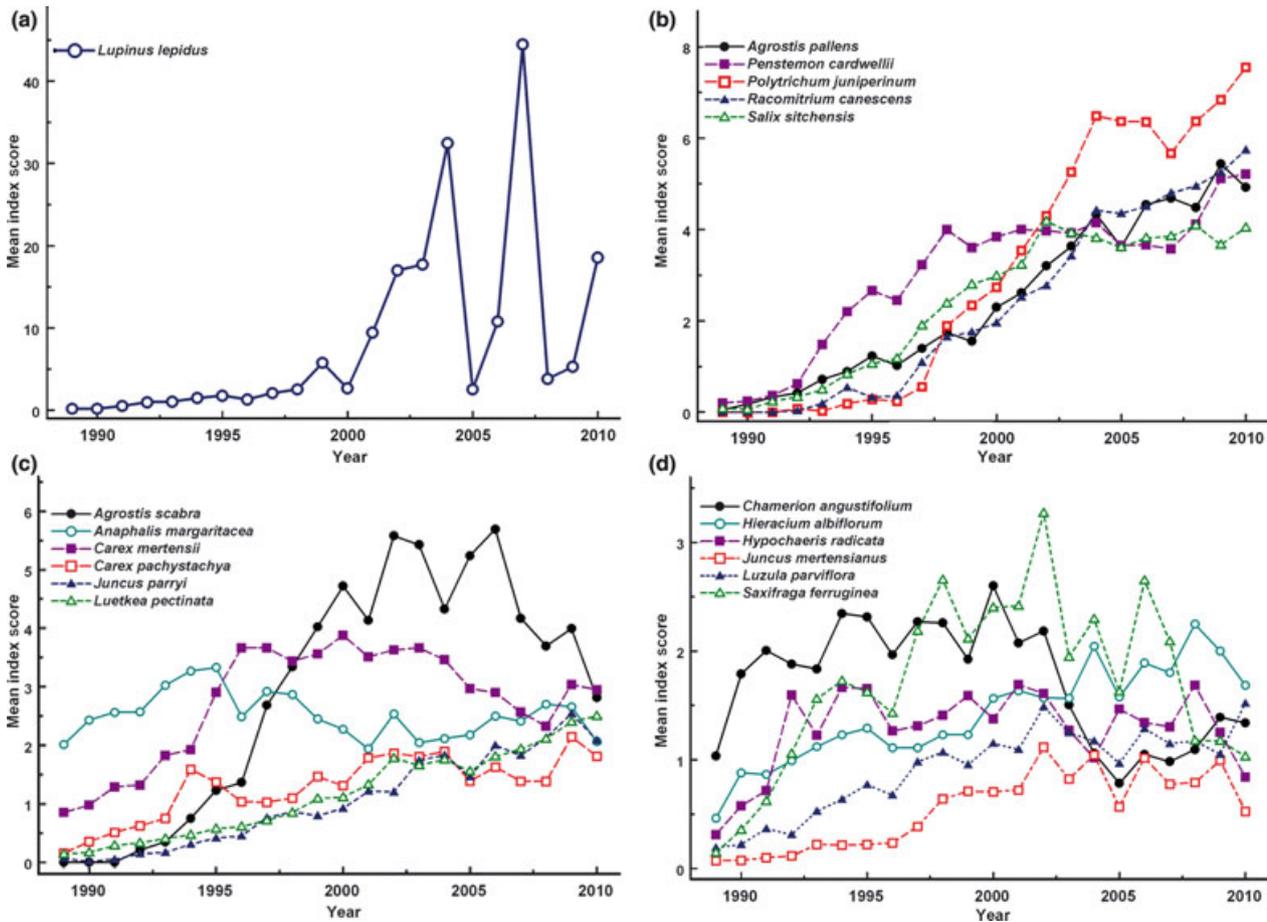
Fig. 3. Species changes: (**a**) *Lupinus lepidus*; (**b**) dominant species, (**c**) common, persistent species, (**d**) less common and short-lived species.
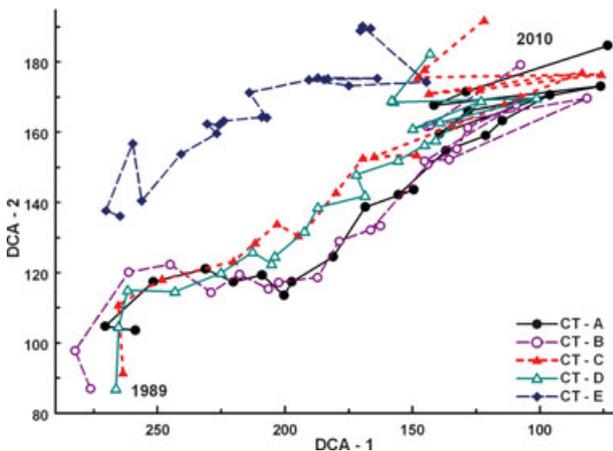

Fig. 4. DCA trajectories for the five community types.

To assess how trajectories of the primary plots developed, we compared Euclidean distance based on DCA-1 and DCA-2 scores for plots grouped spatially (SG) and by habitat type. Linear regression of the running mean of dis-

tances between spatial groups suggested divergence of SG-G (exposed plots) from SG-A ($P < 0.03$, $r^2 = 0.22$), SG-C ($P < 0.02$, $r^2 = 0.28$) and SG-D ($P < 0.001$, $r^2 = 0.48$), all protected plots. Plots in SG-G developed more *Salix* and *Agrostis scabra* than the lower plots. Seven of 28 comparisons converged: SG-B with SG-F ($P < 0.005$, $r^2 = 0.33$) and SG-H ($P < 0.003$, $r^2 = 0.37$), which have similar degrees of slope and protection; SG-C with SG-F ($P < 0.05$, $r^2 = 0.21$) and SG-H ($P < 0.03$, $r^2 = 0.22$), which are exposed; and three pairs of upper grid plots that have similar habitats with lower vegetative cover. SG-E converged with SG-F ($P < 0.02$, $r^2 = 0.28$), while SG-G converged with SG-F ($P < 0.0001$, $r^2 = 0.62$) and SG-H ($P < 0.002$, $r^2 = 0.40$).

A similar analysis between pairs of the five primary habitat types suggested floristic convergence in six of ten comparisons. HT-A converged floristically with HT-C ($P < 0.02$, $r^2 = 0.26$) and HT-D ($P < 0.0001$, $r^2 = 0.61$); HT-B converged with HT-D ($P < 0.02$, $r^2 = 0.26$) and HT-E ($P < 0.005$, $r^2 = 0.34$); HT-C converged with HT-D ($P < 0.02$, $r^2 = 0.24$); and HT-D converged with HT-E ($P < 0.0003$, $r^2 = 0.48$). HT-A, HT-C and HT-D had similar

Table 4. Temporal changes in SDs of detrended correspondence analysis determined by linear regression. Plots grouped by CTs, spatial patterns (SG) and habitat types (HT). Coef. = linear regression coefficient.

Community	SD-DCA-1			SD-DCA-2		
	$P <$	r^2	Coef.	$P <$	r^2	Coef.
CT-A	0.001	0.406	−1.08	0.001	0.467	−0.46
CT-B	0.001	0.463	−1.24	0.001	0.422	−0.55
CT-C	0.02	0.273	−0.62	0.002	0.397	−0.51
CT-D	0.02	0.273	−0.51	0.001	0.451	−0.57
CT-E	NS	0.053	−0.27	0.001	0.806	−1.44
Space						
SG-A	0.05	0.179	−0.368	NS	0.01	0.03
SG-B	0.001	0.392	−1.468	0.05	0.21	−0.28
SG-C	0.001	0.393	−0.957	0.05	0.26	−0.38
SG-D	0.01	0.295	−0.842	NS	0.01	−0.04
SG-E	0.001	0.651	−0.837	NS	0.04	0.06
SG-F	0.05	0.229	−0.252	NS	0.04	0.09
SG-G	0.001	0.648	−1.548	NS	0.11	−0.22
SG-H	0.001	0.729	−1.605	0.01	0.32	−0.21
Habitat						
HT-A	0.01	0.301	−0.82	NS	0.02	0.12
HT-B	0.01	0.418	−1.19	NS	0.01	−0.09
HT-C	0.001	0.423	−0.94	NS	0.01	−0.07
HT-D	0.01	0.274	−0.49	0.01	0.34	0.43
HT-E	0.001	0.694	−1.21	NS	0.06	0.13

Table 5. Convergence between pairs of groups determined by spatial patterns (SG) and habitat types (HT) determined by linear regressions of the 3-yr running mean of the percentage similarity between each pair. All significant results imply floristic convergence.

Comparison	$P <$	r^2	Similarity (%)	
			Early	Late
SG-A →SG-B	0.02	0.28	80	87
SG-A →SG-H	0.0001	0.55	47	77
SG-B →SG-C	0.05	0.20	70	77
SG-B →SG-D	0.003	0.37	66	80
SG-B →SG-E	0.04	0.20	67	72
SG-B →SG-G	0.0001	0.79	59	75
SG-B →SG-H	0.0001	0.75	52	81
SG-C →SG-D	0.0001	0.56	73	82
SG-C →SG-E	0.02	0.28	71	80
SG-C →SG-G	0.02	0.24	75	80
SG-C →SG-H	0.001	0.42	65	81
SG-D →SG-E	0.03	0.20	65	79
SG-D →SG-G	0.02	0.25	70	81
SG-D →SG-H	0.0001	0.58	64	82
SG-G →SG-H	0.0001	0.60	71	80
HT-A→HT-B	0.0001	0.72	79	89
HT-A→HT-C	0.01	0.31	82	92
HT-A→HT-D	0.0001	0.71	75	90
HT-A→HT-E	0.002	0.41	82	91
HT-B→HT-C	0.0001	0.54	79	88
HT-B→HT-D	0.0001	0.67	74	87
HT-B→HT-E	0.0001	0.67	77	92
HT-C→HT-D	0.0001	0.58	75	90
HT-C→HT-E	0.0005	0.46	83	90
HT-D→HT-E	0.0001	0.61	81	89

exposure and soil. While the soils of HT-B, HT-D and HT-E were similar, HT-E was more exposed. HT-C and HT-D were similarly exposed and had similar soil properties. HT-D was more protected than HT-E. These DCA scores converged due to the expansion of persistent species such as *Juncus parryi* and *Penstemon cardwellii* that tolerate most conditions on the grid.

We calculated the percentage similarity annually within each SG and HT and assessed changes in similarity and SD using linear regressions. We compared changes in similarity between spatial groups using the 3-yr running average. They converged in 15 of 28 comparisons, while none diverged. SG-B and SG-C converged with most other groups; SG-F, which is the most exposed, did not converge with any group. Trends are irregular and affected by large variation in *Lupinus* cover. Convergence was driven primarily by the development of mosses, *Juncus*, *Lupinus* and *Penstemon*.

Comparisons of the similarities among HTs revealed convergence in each case (Table 5). Early similarity values were high, but this is a result of lumping plots with different species composition and because the index used obscures significant differences. Nevertheless, overall similarity increased significantly.

Community patterns in space and time

We used Mantel tests to explore control of species pattern. The test used 2010 data and the 48 most common species

to compare distance matrices derived from species and environmental factors. We determined the set of variables that provided the best correlation by trial and error. The best result (Mantel $r = 0.47$; $t = 12.9$; $P < 0.0001$) was achieved using only autogenic factors (gravel, sand, fines, residual soil, exposure, solar radiation and topography). Adding allogenic factors reduced the score. In contrast, using all factors provided substantially reduced power ($r = 0.20$).

Canonical relationships between species composition and explanatory variables should increase during succession. We used explanatory data collected in 2010 to the species matrices of each year to determine: (1) if factors associated with variation changed over time; (2) if overall explained variation increased over time; and (3) if allogenic (spatial) or autogenic (environmental) factors dominated. Allogenic factors were east–west position, elevation (a positional factor at this scale) and distance from relict plots. The other variables were autogenic.

RDA permits an assessment of associations between species composition and explanatory variables. Using RDA, 25.1% of the variation in 2010 was explained (Axis 1 and all canonical axes were significant, $P < 0.0001$). Axis 1

explained 53.5% of the species to environment relationship ($r = 0.819$); Axis 2 explained 18.0% ($r = 0.675$). Canonical coefficients, their t-values and inter-set correlations suggested that exposure to wind ($r = -0.73$), topography ($r = 0.63$), distance from relict sites ($r = -0.62$), relict type ($r = 0.60$) and elevation ($r = -0.45$) were the best predictors. The plots, categorized by CT, form a detectable pattern in relation to the explanatory variables (bi-plot, Fig. 5). CT-E is an outlier whose plots occurred in gullies. Other CTs tended to cluster in their own portion of the graph, but with significant variation.

The overall analysis suggested that similar variables were associated with species composition over time (Table S2). Exposure and elevation were significant early and late in the study, elevation dominated from 2001 to 2007 when *Lupinus* expanded dramatically. Silt fraction was sometimes important. Topography, relict type and distance from relicts sometimes had higher correlations, consistent with the 2010 results. When covariate analysis was used (Prach et al. 2007), autogenic factors consistently explained more variation than did allogenic factors (Fig. 6). Exposure and topography were the leading predictors in most years. Relict type, correlated to topography, was occasionally among the top autogenic variables. East–west position was the dominant allogenic factor in most years after 1991.

Explained variation increased from 1989 to 1992 in each analysis, then fluctuated around 24% for the combined analysis, with a spike of 30.8% in 2004. Autogenic and allogenic variation tracked total variation, and their combined values exceeded that of the combined analysis. We expected this result because some allogenic variables may contain autogenic information and some autogenic variables may express allogenic relationships (e.g. relicts).
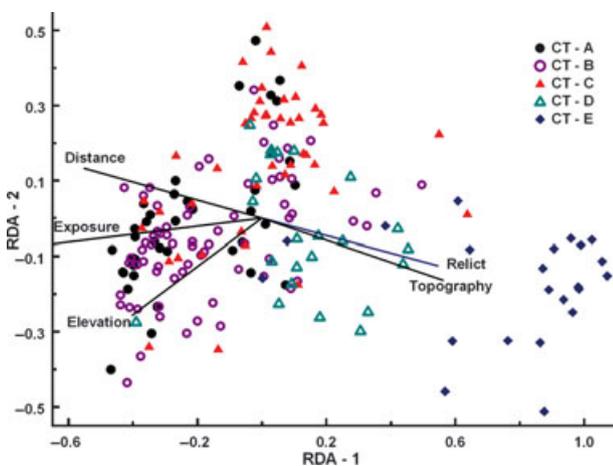

Fig. 5. Redundancy analysis bi-plot. Symbols indicate location of plots determined by the environmental variables. Vectors indicate the relative strength of five important variables; vector lengths multiplied by three for clarity.
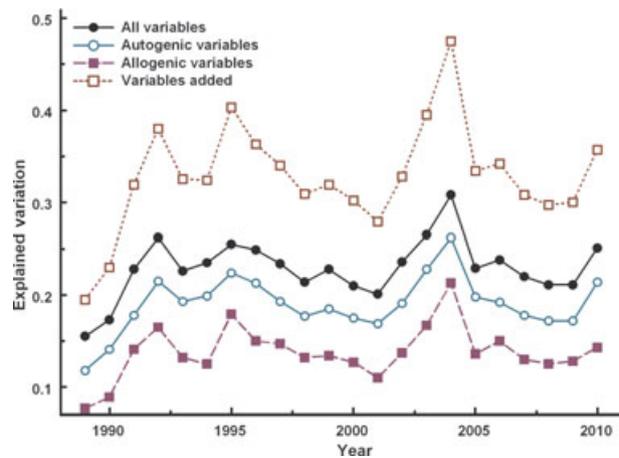

Fig. 6. Explained variance over time determined by redundancy analysis, with 'variables added' being the summation of the covariance analysis.

Lupinus causes pronounced shifts in the species pattern. We conducted a complementary set of analyses. First, all N-fixing species were excluded (*Lupinus*, *Alnus*) from the species matrix. Then a surrogate fertility variable, using the square-root transformed total cover of these species, was added to the explanatory matrix. The correlations were similar to those of the basic analysis, but did not drop during *Lupinus* pulse years (e.g. 2002, 2007).

Discussion

This study is concerned with succession rates, the nature of succession trajectories, the relative importance of allogenic and autogenic explanatory variables and implications for applied vegetation sciences such as restoration. The scale of the study is small, and the study plot represents only a fraction of the existing variation on the Pumice Plain (see del Moral & Lacher 2005), but it does incorporate significant variation.

Rates

Succession rates vary among habitats (Elias & Dias 2009), disturbance types (Butler & Kielland 2008) and during succession (Oksanen & Tonteri 1995). Rates usually slow as persistent species replace short-lived ones (Anderson 2007). Turnover on the Pumice Plain was sufficiently fast that permanent plots could effectively describe succession rates.

Early vegetation assembly had ceased by 2004, as evidenced by stable richness and few new immigrants. Vegetation has matured and cover has expanded to occupy available space. Thus, a competitive phase is developing, in which dominance hierarchies have emerged. Rarer species are disappearing and H′, after initial increases, has declined. These changes imply that a transitory stasis has

existed since 2004. Since then, the fluctuations of *Lupinus*, which enhances fertility (Titus 2009), have dominated succession. Stem borers (*Cryptorhynchus lapathi*) have caused high mortality to *Salix* populations, whose cover has remained unchanged since 2002 despite substantial recruitment. A shortage of mycorrhizae or summer drought may limit conifers. Although conifer seedlings recur, few have reached 2 m in height. We predict that the pace of succession will accelerate and converge further once conifers or *Salix* can establish.

Mosses continue to expand, particularly in response to *Lupinus*. Persistent species, including *Agrostis pallens*, *Penstemon cardwellii*, *Luetkea pectinata* and *Juncus parryi*, continue to increase episodically. Pioneer species such as *Anaphalis margaritacea*, *Chamerion angustifolium* and *Hypochaeris radicata* are in decline, which should counter the increasingly static condition.

Community types on primary surfaces expressed similar rates of change, but the relict CT-E was much slower. This suggests the importance of surviving vegetation in directing trajectories, ameliorating species composition changes and retarding succession.

Regressions of changes in DCA positions on time implied fitful slowing of succession. This is a common result in chronosequence studies (Robbins & Matthews 2009) and in permanent plot studies (del Moral et al. 2010). Because *Lupinus* has varied wildly since 2004, mean rates were difficult to assess; however, Euclidean distances from year to year declined, supporting the conclusion of reduced floristic change over time. The rate may again accelerate during a transition to tall shrubs and conifers, and then again decline due to increased species longevity.

Convergence

Succession trajectories have been discussed thoroughly (Walker & del Moral 2009); the usual expectation is that vegetation will converge as it matures (Matthews et al. 2009) because habitats become homogeneous as vegetation develops (e.g. Anthelme et al. 2007). However, divergence may occur if uniform sites develop distinctive features (Bossuyt et al. 2003), if priority effects lead to unique trajectories (Abella & Denton 2009; Lanta & Lepš 2009), if stochastic colonization creates floristic heterogeneity (Dolezal et al. 2008; del Moral et al. 2010) or if subsequent disturbances create mosaics (Tsuyuzaki 2009). Chronosequence studies are likely to suggest convergence under strong competitive pressures (Navas & Violle 2009) or after life-form changes (Lepori & Malmqvist 2009). However, permanent plot studies often find divergence (cf. Fastie 1995; Baeten et al. 2010).

It is possible for adjacent vegetation samples to be dissimilar if the components are persistent and can resist inva-

sion (Huisman et al. 2009; Odion et al. 2010). Such priority effects appear on this grid. For example, in the northeast corner of the grid, CT-A plots persistently differ from adjacent CT-C plots in having more *Lupinus* and less moss cover. High *Salix* and low *Lupinus* distinguish a CT-D plot in Row 13 from surrounding plots. These floristic differences serve to emphasize the importance of persistent species in guiding local trajectories. Intrinsic habitat differences also contribute to maintaining distinct communities.

Vegetation on primary surfaces became less variable over time whether we grouped plots by floristic, spatial or habitat criteria. Standard deviations of four CTs declined significantly in both dimensions, while SD of CT-E declined only in DCA-2. Internal floristic variation was reduced, but in 2010, it still ranged from 0.13 to 0.21 half-changes. Thus, convergence is incomplete and constrained by habitat variations, subsequent disturbances, priority effects, herbivory and other factors. Further convergence may develop when biotic interactions increase dominance.

Comparing trajectories using differences in mean DCA positions is problematic because scores are sensitive to large species fluctuations and because comparisons are limited to a few dimensions. Using linear regression may obscure trends. Using percentage similarity is marginally better, although interpretations of linear regressions remain problematic due to annual variations in species composition. These analyses do imply that vegetation in this small sample of primary succession is becoming more homogeneous as different samples become internally more homogeneous and increasingly similar to other samples. However, there is a limit to convergence on this grid. Different habitats will continue to support at least moderately different species assemblages. Spatial groups will continue to reflect different habitats.

Allogenic and autogenic variables

Whittaker (1993) not only suggested that stochastic, allogenic factors are paramount in early primary succession, but that tighter species–environment ties develop. This conjecture is hard to demonstrate since opportunities to explore how autogenic factors control the development of vegetation are rare. Even in ideal situations, much variation remains unexplained, in part due to the difficulty of measuring relevant variables. Thus, we cannot expect large explained variation even as competition and other autogenic factors edit species composition. In addition, priority effects that result from allogenic factors and local disturbances due to herbivory (Eskelinen & Viranen 2005) or unusual weather can decouple vegetation from autogenic factors.

Autogenic and allogenic factors are not always distinct. Elevation effectively described species variation on a

landscape-scale study of a lahar on the east slope of Mount St. Helens (del Moral et al. 2009). This was related to growing season effects and to position. In this case, an elevation range of only 32 m, it is strongly correlated to the row variable and has little effect on temperature at this scale. For this reason, we consider elevation to be an allogenic factor. Hence, autogenic factors may be correlated with allogenic factors (see Fig. 6).

On Mount St. Helens several studies have demonstrated shifts from allogenic to autogenic control of vegetation (e.g. del Moral et al. 2010). On the Pumice Plain, explained variance increased from 15% (del Moral et al. 1995) to 28% in 2004 (del Moral & Lacher 2005). On the east flank of Mount St. Helens in 2007, 80% of the explained variance was spatial (del Moral et al. 2009), but that study sampled vegetation over a significant elevation range and at varying distances from intact vegetation. In a detailed longitudinal study of variation within specialized microsites near the Pumice Plain grid ('potholes'), del Moral (2009) found that autogenic factors had increased four-fold while allogenic factors had changed little over 15 yrs.

Mantel tests suggested that autogenic factors explained most variation on the grid, but that allogenic factors were also significant. RDA supported and clarified the Mantel analyses. Explained variance in 2010 was lower than the peak obtained in 2004 when *Lupinus* suppressed much of the vegetation variation, and modest compared to other sites on Mount St. Helens.

Comparing the data across 22 yrs provided two surprises. While Baasch et al. (2009) showed that relationships between vegetation and explanatory variables increased over time and spatial effects declined, we found that autogenic factors were consistently more important than allogenic factors, their proportion did not change and there was no sustained increase in explained variation after 1992. Peak correlations to the first species axis reached 0.85 by 1995 and then fluctuated. This result suggests that priority effects may arrest further development of predictive relationships. When a nitrogen surrogate was included, after deleting N-fixing species, correlations fluctuated little, showing the importance of *Lupinus* to the dynamics of this system. The summation of variation explained by autogenic and allogenic factors always substantially exceeded that in the complete analysis, indicating that there is redundant information. In this case, elevation combines allogenic (e.g. through dispersal effects) and autogenic (e.g. through temperature effects) components. The annual studies varied slightly over the years, but consistently indicated that exposure and topography dominated the autogenic factors, while east–west location dominated allogenic factors after 2001. The last appears to reflect greater moisture and greater fraction of relict plots. Controlling factors changed little over time,

although variation in *Lupinus* affects the details. The overall explained variance did not increase significantly after 1995 and peaked (30%) before the conclusion of this study. The scale of this study limited the relative importance of allogenic factors and, contrary to the expectation of Whittaker (1993), relationships between autogenic and allogenic factors remained unchanged.

Three autogenic factors (exposure, topography and relict type) and two allogenic ones [elevation (row position) and distance from relicts] were the best predictors in RDA. Each applies to the entire plot. Factors such as moisture were from a single point and were unlikely to reflect typical species composition. It appears that the habitat variation that controls species composition relates to effective moisture (estimated by exposure, radiation and soil factors).

Implications

This study suggests that succession may not proceed without fits and starts because it results from the combination of many interrelated components. Unmeasured factors, such as herbivory, few mycorrhizae and browsing by elk, have differential effects that may lead to unpredictable consequences. The importance of survivors in relict sites was reinforced, as was the importance of subtle habitat differences in maintaining distinct communities.

That communities have remained distinct in a relatively homogeneous habitat, even though they are becoming more similar, suggests that alternative stable states may be more common than is generally appreciated. Therefore, when restoring damaged habitats one should plan for acceptable alternatives to promote habitat variability that can enhance biodiversity, resistance to stress and resilience (del Moral et al. 2007; Walker & del Moral 2009). That there appears to be a limit to the degree to which species and local environments are linked, suggests that there are multiple opportunities for creative management of recovering landscapes. Similar environments can support variable vegetation, depending mainly on the time of establishment and disturbance regimes, which are under the control of restoration ecologists. On this example of primary succession on pumice, links between species and their environment have remained constant over many years, suggesting that priority effects are strong. During restoration, early planting of characteristic species is likely to be effective.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Species encountered on the Pumice Plain grid (1989–2010).

Figure S1. Pumice Plain study area. a) 1989 of site immediately above the grid; b) 2010, dominated by *Lupinus lepidus* with *Penstemon* and *Salix* scattered on the landscape.

Figure S2. Pumice Plain study area. a) 2007, dominated by *Lupinus lepidus*, with scattered *Agrostis* and *Carex* in the matrix and Mount St. Helens in the background; b) 2007, *Salix* and *Abies* are in the middle distance and Spirit Lake is in distance.

Table S1. Summary of RDA over 22 yrs. Auto = autogenic variables; Allo = allogenic variables; All is correlation using all selected variables; Corr = correlation. Factor abbreviations (see also Table 1): exp = exposure to wind; topo = topographic features; elev = elevation; east = longitude; relict = degree of residual soil; rel. dist = distance from relict plots.

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