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Increasing deterministic control of primary succession on Mount St. Helens, Washington

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Abstract

Question: Does the relative importance of stochastic and deterministic factors change during primary succession?

Location: Small depressions (potholes) located on Mount St. Helens, Washington (46°13′51″N, 122°09′10″W, 1290 m).

Methods: Pothole vegetation was described in 1993, 1997 and from 2001 to 2008. Explanatory variables included location and elevation (spatial factors), soil factors and *Lupinus lepidus* cover from prior years (a fertility surrogate). RDA assessed species-variable relationships. DCA calculated β diversity and within-year heterogeneity. Flexible sorting classified the vegetation. Species composition, richness, cover, H′ and evenness were also calculated.

Results: Vegetation cover increased through 2001, and then fluctuated due to changes in *L. lepidus* cover. Richness peaked in 2005, after which pioneer species began to decline as persistent evergreen species increased. The six CTs recognized in 2008 were more scattered than were the six different CTs from 2001. DCA demonstrated that woody and rhizomatous species increased as pothole vegetation became less variable. RDA revealed weak spatial relationships in 1993, 1997 and 2001; thereafter, environmental and biological factors became important. The species-explanatory data relationship increased during this study from 10.2% to 36.0%, leaving 64.0% of the variation unexplained.

Conclusions: This is the first temporal study to demonstrate that deterministic control of vegetation development increases during succession. Pothole vegetation has converged somewhat due to deterministic factors, but the initial effects of chance, local disturbances and history remain large and may prevent strong convergence.

Keywords: Biological filters; Community assembly; Convergence; *Lupinus lepidus*; Redundancy analysis; Stochastic assembly.

Nomenclature: Determined from the USDA Natural Resources Conservation Service: http://plants.usda.gov/index.html checked June 22, 2009

Introduction

Understanding how communities assemble should allow greater success in restoring vegetation after devastating impacts (Walker & del Moral 2003). While early assembly of species appears stochastic, there is disagreement about the subsequent importance of assembly rules and determinate processes (Lepš & Rejmánek 1991). Deterministic factors are those that can be measured or inferred to predict species patterns. They include soil properties and processes such as competition, facilitation and grazing that can filter species responses. Other variation may be due to stochastic timing between variable events (e.g. summer rainfall) and phenology, unique events (Velazquez & Gomez-Sal 2008), unmeasured critical variables, sampling error and poor models (McCune & Allen 1985). Proximity to potential colonists can be stochastic (del Moral & Ellis 2004; Bischoff et al. 2009). Alternative results may result from the same factors (Walker & del Moral 2009); for example, isolation from potential colonists alone can produce different species composition (del Moral & Eckert 2005). Priority effects can generate stable yet immature vegetation (Trowbridge 2007), but deterministic environmental factors, herbivory, facilitation or competition can override stochastic factors to produce predictable communities. During succession, factors such as soil moisture (Battaglia & Collins 2006), pH (Prach et al. 2007) and texture (Dolezal et al. 2008) may alter species composition, while biotic interactions can promote community convergence (Ejrnaes et al. 2006).

Microsites promote establishment during succession (Jumpponen et al. 1999), but biotic effects and microsite modifications reduce species variability and can improve predictability of species composition (del Moral & Ellis 2004). No community forms solely from stochastic processes or deterministic filters (Lord et al. 2000), but the balance may shift in time. Therefore, the question is, "Does the relative importance of stochastic and deterministic factors change during primary succession?" To seek an answer, I explored deterministic factors in small depressions (potholes) found on Mount St. Helens. I propose that at a local scale, deterministic factors gradually become more evident with time (cf. Cutler et al. 2008).

Methods

Study site

Several hundred potholes developed on the northeast slope of Mount St. Helens during its eruption (18 May 1980; Fig. 1). They centre at 46°13′51″N, 122°09′10″W, (UTM84 easting 10T 56 4842, northing 511 9985), between 1269 and 1308 m a.s.l. They covered 6 ha and each contained an independent sample of the seed rain. Selected potholes had intact rims, so there was no drainage. Potholes were 29.6 ± 7.0-cm deep, with an average area of 27.3 ± 14.5 m^2 (8.9-84.4 m^2).

Vegetation sampling

In 1993, I determined cover of all plants within 111 potholes (del Moral 1999); most were re-sampled in 1997, together with additional potholes ($n = 117$). Accurately locating potholes only became possible in 1999, and some potholes could not be relocated. From 2001 to 2007, percentage cover of all plants in 105 potholes inventoried in 1993 and 1997 was measured. In 2008, I selected 80 of these potholes after excluding the largest, smallest, those adjacent to others and those no longer intact. The cover of each species was sampled in four 1-m^2 quadrats separated by 15 cm. Since the 2001 to 2007 inventories covered larger areas than the 2008 4-m^2 sample, they included more species, microsites and bare space. I used these 80 potholes to describe vegetation from 2001 to 2007. Species encountered in this study are listed in Appendix 1.

Explanatory variables

Explanatory data were soil properties, location and *Lupinus* cover. In 1993 and 1997, location was determined from a grid, and elevation was relative and approximate; thereafter, GPS co-ordinates defined position and elevation. Potholes were from 376 to 593 m from sources of potential colonists, such that distance was not relevant (del Moral & Lacher 2005).

Prior to 2008, two 200-g soil samples were obtained from depths of 4 to 8 cm near the centre of each pothole. In 2008, one 200-g soil sample was similarly obtained from the centre of each quadrat. In each year, percentage soil moisture was determined gravimetrically. Because soil pH can affect species composition (Prach et al. 2007), it was determined from a 1:1 soil:water paste. Soil organic matter was estimated using a 10-g portion of each soil sample (dried at 400°C for 24 h). Soil texture was determined by sieving 100-g samples. Texture classes were rocks (did not pass through a 4.75-mm screen), gravel (2-mm screen), sand (250-μm screen) and fines (passed through all screens). Sand fractions were excluded to avoid autocorrelation.

I used *L. lepidus* cover from 2004 to 2007 as a proxy for soil fertility in 2008 because it is a potent nitrogen fixer; where *Lupinus* cover was dense, soil nitrogen quadrupled (Halvorson et al. 2005). *Lupinus* cover for 2006 to 2008 was excluded in the 2006 analysis and no *Lupinus* data were used in RDA of prior years. *Lupinus* was sparse in 1993 and averaged <1% in 1997. It has undergone two abundance cycles, averaging 22% (coefficient of

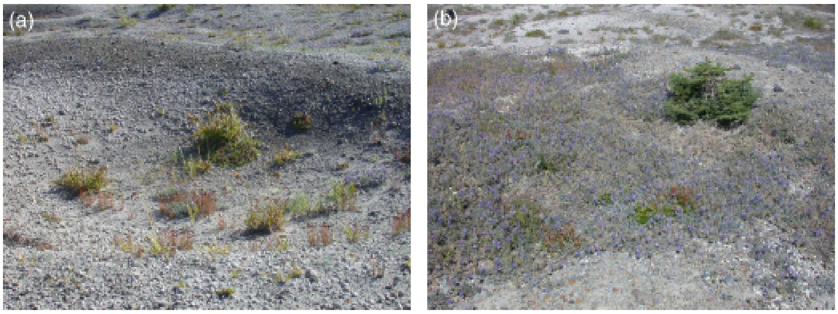

Fig. 1. Typical potholes. (**a**) 2002 with mixture of species including *Lupinus lepidus*, *Anaphalis margaritacea*, *Juncus mertensii* and *Carex* spp. (**b**) 2002 potholes dominated by *L. lepidus*, with *Anaphalis*, *Penstemon cardwellii* and *Abies* sp.

variation = 91.3), 0.3% (CV = 109.3), 1.0% (CV = 129.9) and 8.5% (CV = 93.5) from 2004 to 2007. While *Lupinus* cover in the current year is linked to its previous cover, the values are not closely linked. Spatial explanatory variables were position (UTM coordinates) and elevation (digital topographic map; National Geographic Society 2008).

Analyses

Before 2008, all vegetation of each pothole was measured, providing one value for each species. In 2008, the mean percentage cover of each species in the four quadrats was used. Percentage cover was used to calculate the Shannon diversity index ($H' = [-\Sigma p_i \log p_i]$) and equitability [$E = H'/\ln(\alpha)$], where p_i is the proportion of cover represented by the ith species and α is the number of species (McCune & Mefford 2006).

I classified the 2008 plots into community types (CTs) using flexible sorting of Euclidean distance ($\beta = -0.25$). I used principal components analysis (PCA) to visualize relationships among the potholes (ter Braak & Šmilauer 2007). Both samples and species were centered and standardized, and species scores were square-root-transformed. I used redundancy analysis (RDA) (ter Braak & Šmilauer 2007) to explore the relationship between species composition and the explanatory variables. RDA was used because there were relatively few empty cells in the species matrix, and species distributions appeared to be linear. PCA was applied to the square-root-transformed cover. RDA standardizes explanatory variables to eliminate scaling differences. The correlation of explanatory variables to the RDA axes estimated its relationship to vegetation. *T*-values suggest the significance of the regression coefficients ($df = 80$ samples − 12 variables − 1 = 67). The significance of variation was determined by comparing the result to a null model derived from 2000 trials of randomized explanatory variables.

I used detrended correspondence analysis (DCA) (PC-ORD 5; McCune & Mefford 2006) of samples from 1993 to 2007 to assess β diversity (Oksanen & Tonteri 1995). Mantel tests were used to compare matrices of Euclidean distances of plots in species composition space with those of plots in explanatory variable space. The method provides a *t*-value and the Mantel statistic (***r***). Statistics were conducted with Statistix 9 (Analytical Software 2008). Graphs were produced with Axum 7 (Mathsoft 2001).

Results

Structural development of potholes

The vegetation structure of the potholes changed greatly over time (Table 1). Initially, only some sparsely distributed species occurred. Richness, cover and diversity increased by 1997, and evenness remained high. These changes were correlated to remarkable changes in the abundance of *L. lepidus* (Archive II). *Lupinus* was rare in 1993 (frequency 14%, maximum cover = 0.5%); by 1997, it had expanded (frequency 50.4%) and was locally common (maximum cover = 15.7%); and from 2001 to 2004, it expanded further. Richness increased slightly, cover doubled and diversity declined during this period. Late in 2004, leaf miners (*Staudingeria albipennela*) and moths (*Filatima loowita*) devastated the *Lupinus* (Bishop et al. 2005), which allowed other species to expand. *Lupinus* again declined late in 2007 due to pathogens and herbivory (J.G. Bishop, pers. comm.). The cover of short-lived colonists including *Anaphalis*, *Chamerion* and *Hieracium* declined after 1997. Richness, cover of other species and diversity peaked in 2005, after which *Lupinus* reasserted dominance. Species proportions changed dramatically (Appendix 2). Relative cover of species such as *Anaphalis*, *Agrostis scabra* and *Chamerion* declined, while persistent species such as *Agrostis pallens*, *Penstemon*, *Luetkea* and *Racomitrium* increased. The decline of *Salix sitchensis* is related

Table 1. Vegetation structure in potholes. Between 1993 and 2007, the total area of each pothole was completely inventoried. The 2008 data are from a 4-m^2 sample. Differences among means in years 2001 through 2007 were determined by repeat measures analysis of variance, followed by a Bonferroni test of differences. The effects of "Year" were all highly significant ($P < 0.0001$). Superscripts indicate means that are significantly different ($P < 0.05$). Excluded from the comparisons were 1993 and 1997 samples (a somewhat different set of potholes) and the 2008 sample (different sampling method with smaller area).

Year (*n*)	*Lupinus* (%)	Richness	Cover (%)	H'	Evenness
1993 (111)	0.02	8.6	2.5	1.506	0.713
1997 (117)	0.96	12	10.6	1.824	0.743
2001 (80)	9.84^{b}	13.2^{b}	19.1^{a}	1.757^{cd}	0.683^{bc}
2002 (80)	18.1^{cd}	13.0^{b}	26.0^{bc}	1.460^{a}	0.576^{a}
2003 (80)	14.8^{bc}	14.2^{c}	28.6^{c}	1.604^{a}	0.608^{a}
2004 (80)	22.2^{d}	14.5^{b}	37.8^{d}	1.517^{a}	0.571^{a}
2005 (80)	0.32^{a}	16.5^{d}	28.5^{c}	1.986^{d}	0.709^{c}
2006 (80)	1.03^{a}	14.9^{c}	20.7^{ab}	1.858^{cd}	0.689^{bc}
2007 (80)	8.47^{b}	12.1^{a}	28.6^{c}	1.566^{a}	0.632^{ab}
2008 (80)	7.63	11.8	44.6	1.700	0.693

primarily to an introduced stem-boring beetle (*Cryptorhyncus lapathi*, J.G. Bishop, pers. comm.).

Community types

The 2008 data were classified into six CTs. While potholes within a CT were spatially dispersed, there was some aggregation (Fig. 2). However, potholes assigned to different CTs often intermingled, and mean positions of the CTs were indistinct. PCA of the 2008 samples demonstrated the validity of the CTs (Fig. 3). This analysis accounted for 48.7% of the variation on the first two axes.

CT-A (*Agrostis pallens*-*Racomitrium canescens*) was sparse; *Penstemon cardwellii* was common; and *L. lepidus* occurred but was not abundant. CT-B (*Racomitrium*-*Lupinus*-*Agrostis*) was dominated by the most common species in the study, together with *Carex mertensii, Penstemon* and *Juncus parryi*. CT-C (*Agrostis*-*Lupinus*-*Racomitrium*) was similar to CT-B, but the proportions of the dominants differed and there was little *Penstemon*. CT-D (*Penstemon*-*Agrostis*-*Juncus*) was sparsely vegetated, but diverse, dense *Rumex acetosella*, an introduced species, occurred sporadically. CT-E (*Penstemon*-*Lupinus*-*Agrostis*-*Polytrichum juniperinum*) also had *Salix sitchensis* and *Hieracium albiflorum*. CT-F (*Lupinus*-*Polytrichum*-*C. mertensii*) had little *Racomitrium*, but *Penstemon* and *Hieracium* occurred consistently.

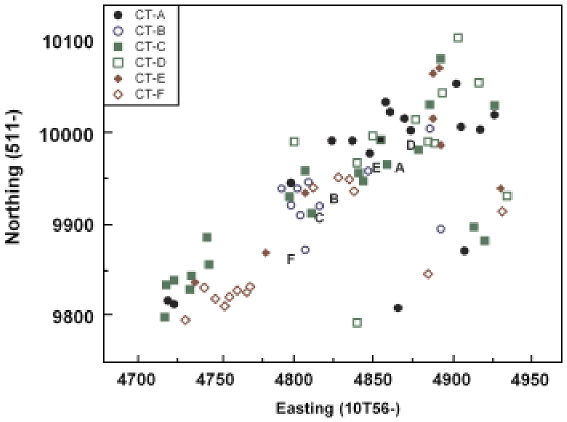

Fig. 2. Distribution of sample plots in the landscape. Symbols refer to classification into six CTs. Letters indicate spatial centroids for each CT. (The gap is a deep ravine separating the sample field. Because the potholes straddle the northing transition from 511 to 512, it was adjusted.)

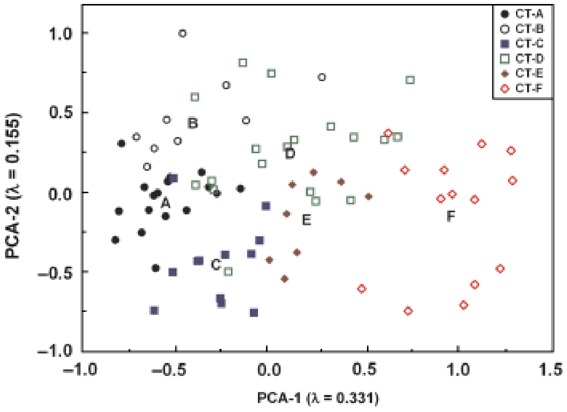

Fig. 3. Distribution of sample plots determined by principal components analysis. λ = eigenvalue for the two axes.

Table 2. Community types determined by agglomerative clustering (Sørensen's distance metric with flexible sorting, $\beta = -0.25$). Differences between means in a column were determined by ANOVA, followed by Bonferroni comparisons ($P < 0.05$).

CT	N	Richness	% Cover	H'	Evenness
A	17	11.5	34.4^{b}	1.713^{ab}	0.703^{ab}
B	10	11.2	50.5^{ab}	1.569^{b}	0.650^{ab}
C	19	11.8	45.3^{b}	1.591^{b}	0.649^{b}
D	12	11.7	33.2^{b}	1.844^{a}	0.756^{a}
E	8	13.0	43.5^{b}	1.931^{a}	0.758^{a}
F	14	11.9	62.4^{a}	1.662^{ab}	0.678^{b}

As vegetation cover increased, H' and evenness typically declined (Table 2); highest cover was in CT-F, dominated by *Lupinus* and *Polytrichum*. There was no geographic pattern to these structural measures. In 2001, pothole data were classified, as in the 2008 sample, into six different CTs. Paired t-tests of the ranked standard deviation (SD) showed that spatial variation of the potholes increased, easting from 40.6 to 56.3 m ($t = 3.35$, $P < 0.03$), and northing from 48.6 to 69.5 m ($t = 4.50$, $P < 0.007$).

Predictability of species composition

Relationships between species distributions and explanatory variables were explored using RDA in 1993, 1997, 2001, 2006 and 2008. The correlation of the first axis (RDA-1) to species pattern increased from 0.597 to 0.774, while only 2008 had an RDA-2 correlation over 0.650 (Table 3). Explained variation increased consistently as useful explanatory variables shifted from spatial to local factors (Table 4). The inter-set correlations of RDA-1 with elevation (and its correlate, Northing), soil texture, *Lup*'04 and *Lup*'05 were each strong. The texture classes and *Lup*'05 had significant t-values. On RDA-2, moisture had a high correlation and large

Table 3. Redundancy analyses of potholes in 1993, 1997, 2001, 2006 and 2008, years for which environmental data were obtained. Overall eigenvalues and overall species–variable relationships used all available variables. Environmental and spatial variables, determined by covariance analysis, estimated the effects of local factors or landscape factors, respectively. Significance of eigenvalues and explained variation: $a = 0.05$; $b = 0.01$; $c = 0.001$.

Characteristic	1993	1997	2001	2006	2008
Overall eigenvalue RDA-1	0.031	0.091^c	0.265^c	0.163^c	0.192^c
Overall species–variable RDA-1	0.597	0.697	0.650	0.770	0.774
Environment eigenvalue RDA-1	0.020	0.024	0.030	0.097	0.084
Environmental variables RDA-1	0.430	0.488	0.292	0.560	0.593
Spatial eigenvalue RDA-1	0.027	0.053	0.081	0.033	0.036
Spatial variables RDA-1	0.569	0.617	0.457	0.638	0.583
Overall eigenvalue RDA-2	0.026	0.023^c	0.011^c	0.059^c	0.077^c
Overall species–variable RDA-2	0.496	0.539	0.45	0.455	0.686
Environment eigenvalue RDA-2	0.110	0.120	0.010	0.037	0.047
Environmental variables RDA-2	0.391	0.462	0.400	0.498	0.640
Spatial eigenvalue RDA-2	0.019	0.013	0.003	0.014	0.014
Spatial variables RDA-2	0.508	0.389	0.345	0.485	0.367
Overall explained variation	10.2	16.2^c	29.7^c	29.6^c	36.0^c
Environmental variation	5.9	6.9	7.5	19.3^a	22.7^c
Spatial variation	4.9^b	7.3^c	11.1^c	7.4	7.2

Table 4. Inter-set correlations between explanatory variables and 2008 species composition, canonical correlations of explanatory variables and the respective significant t-values (sand omitted due to autocorrelation effects). Soil organic matter percentage from 2006. "*Lup*" = *Lupinus lepidus* cover. Variables with no predictive value or inter-set correlations less than 0.45 were omitted.

Predictor	RDA axis 1		t-value	RDA axis 2		t-value
	Inter-set correlation	Canonical coefficient		Inter-set correlation	Canonical coefficient	
Northing	−0.591	−0.147		0.119	−0.133	
Elevation	0.555	0.076		−0.174	−0.013	
Moisture	−0.323	0.045		0.499	0.191	3.90
Soil pH	−0.344	0.019		0.267	0.098	2.21
Rocks	−0.330	−0.170	2.45	0.206	0.027	
Gravel	−0.442	−0.288	−3.31	−0.100	−0.137	
Fines	0.386	−0.180	−2.01	−0.032	−0.063	
Lup'04	0.451	0.091		−0.187	−0.027	
Lup'05	0.515	0.158	2.48	−0.008	0.010	

t-value; soil pH had a significant t-value. These axes accounted for 36.0% of the explained variation.

Bi-plots of the 2008 RDA display the best explanatory variables (Fig. 4a). While potholes of a given CT were often dispersed, their mean position often remained distinct. This was less true for CT-B, CT-C and CT-E than for the other groups. Thus, much variation remained unexplained. The species centroids suggested their relationships to explanatory variables (Fig. 4b), but correlations with explanatory variables were often low. Species strongly related to variables included: *Lupinus* (−moisture, +elevation, −gravel, +*Lup*'05), *Polystichum* (+elevation, +organic %, −gravel, +*Lup*'05), *Agrostis pallens* (−moisture, +elevation), *Hieracium* (+elevation, −pH, −moisture, +fines), *Racomitrium* (−moisture), *Salix* (+moisture) and *Cistanthe* (+coarse, +moisture).

Comparing spatial with habitat variables

A covariance analysis of environmental and spatial variables for each available year was conducted with RDA (Table 3; see Lepš & Šmilauer 2003). In 1993, 1997 and 2001, spatial factors were weak, although they increased, and environmental variables were insignificant. From 2002 to 2004, *Lupinus* abundance exploded. By 2006, environmental predictors were significantly correlated with both axes, explaining nearly 70% of the explainable variation. This trend intensified in 2008, as moisture, *Lup*'05 and *Lup*'04 dominated the explanatory variables. Over 80% of the explainable variation was associated with the environmental factors.

There was a modest Mantel correlation of the 2008 data with all variables (Table 5), but the best relationship occurred using only environmental

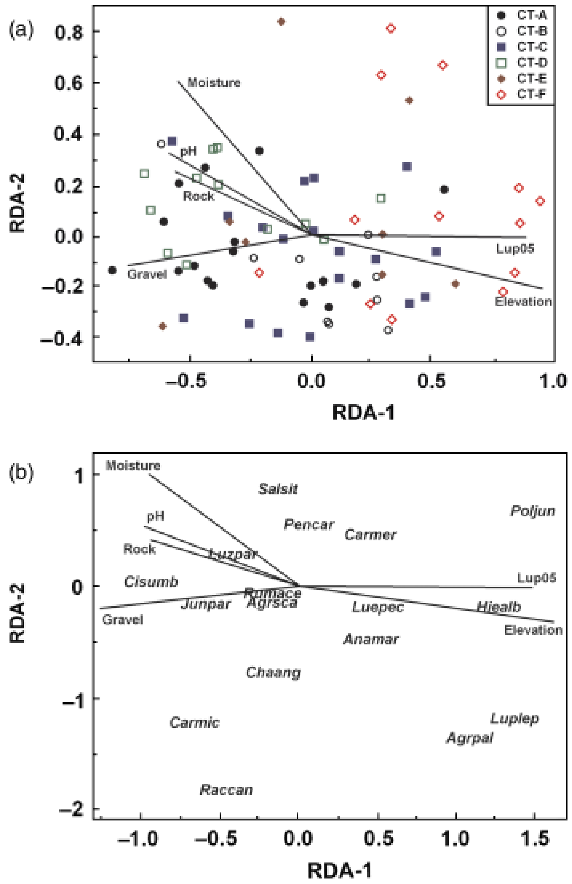

Fig. 4. Redundancy analysis bi-plots (2008 sample). (**a**) Distribution of pothole vegetation in a space determined by species composition constrained by the explanatory variables. The length of the vectors is proportional to the importance of the variable (vector length multiplied by three to improve visualization). (**b**) Mode of species location in relation to explanatory variables (vector length multiplied by five to improve visualization). Species abbreviations can be found in Electronic Appendix 1.

Table 5. Mantel tests of relationships between explanatory variables and species patterns in 2008 (Position is northing and easting).

TRIAL	*n*	Mantel *r*	*t*	*P* <
All explanatory variables	12	0.172	2.86	0.005
Minus position	10	0.195	4.02	6.2E-05
Minus spatial	9	0.269	7.00	1.0E-08
All habitat explanatory variables	6	0.360	9.29	1.0E-09
Minus elevation	5	0.273	5.72	1.0E-08
Lupines alone (4 years)	4	0.301	6.97	1.0E-08
Spatial variables	3	0.1572	2.66	0.008
Position	2	0.1471	2.46	0.014

variables (including elevation) ($r = 0.36$). Environmental variables (excluding elevation) produced a lower correlation, while *Lupinus* alone produced a strong correlation. Spatial factors produced weak, but significant, correlations. The analysis is confounded when variables of little explanatory value are included.

Changing pattern of deterministic intensity

If deterministic control was increasing, then species composition should change predictably. Shorter-lived species such as *Anaphalis*, *Hieracium* and *Chamerion* that dominated sites early in succession should decline, while persistent species such as *Agrostis pallens*, *Juncus*, *Luetkea*, *Penstemon* and mosses should increase. The changes in patterns of absolute and relative cover with time were observed (Appendix 3). Although total cover increased significantly, that of pioneer species (e.g. *Anaphalis*, *Hieracium*, *Chamerion*, *Carex mertensii*, *C. microptera* and *Hypochaeris*) declined, often sharply.

DCA allowed assessment of changes in species composition measured by half-changes (HC; Fig. 5), here scaled as 100 units. To reduce outlier effects, HC was calculated from the difference between the tenth lowest and the tenth highest score. (The 2008 data were excluded because the sampling method differed.) Mean DCA-1 scores declined from 1993 to 2007 and were driven by increases in persistent species (*Agrostis pallens*, *L. lepidus*, *Penstemon cardwellii, Juncus parviflora*, *Luetkea pectinata* and mosses). DCA-2 changed little until 2006. Beta diversity (β) and the SD of DCA-1 scores each declined, which suggested that determinism was increasing. Reduced species variation implies greater dominance and hence stronger biotic effects.

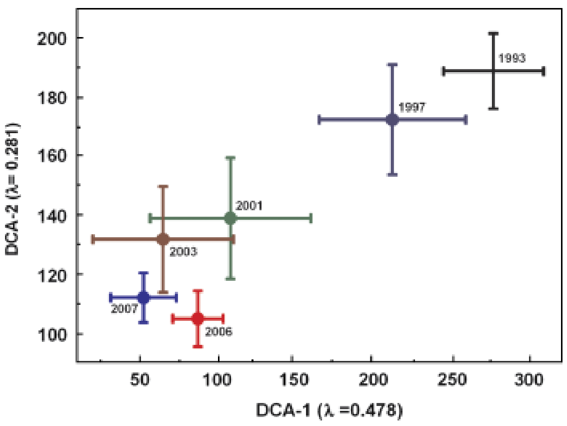

Fig. 5. Mean (± SD) DCA scores 1993 to 2007. SD reflects internal HC in each year.

Discussion

The balance between stochastic and deterministic processes in succession has been long debated. Stochastic processes have been explored with null models (Hubbell 2001), distance (Bossuyt et al. 2003), contingencies (Bakker & Moore 2007) and climate variation (MacDougall et al. 2008). Determinism has been studied as niche assembly (Lepori & Malmqvist 2009), environmental determinism (Sesnie et al. 2009) and biotic filters (Jentsch et al. 2009). Earlier studies on Mount St. Helens suggested that stochastic dispersal dominated early succession (del Moral et al. 2005); now it appears that more predictable habitat and biological filters are developing.

Since 1993, the explanatory value of local variables increased in this site. Potholes are less stressful sites and trap more seeds than the surrounding sites, allowing succession to proceed more quickly. Lower stress promotes more cover and diversity than on barrens. In 1998, barrens averaged 4.3% cover compared to 10.6% in potholes (del Moral & Jones 2002); while in 2002, barrens averaged 9.0% cover versus 26.0% in potholes (del Moral & Eckert 2005). Yet dominance hierarchies were similar to those of adjacent permanent plots ($r = 0.84$ $P < 0.0001$, unpublished). *Lupinus* and mosses were less prominent in potholes, while less stress-tolerant species (e.g. *Arnica latifolia*, *Rumex acetosella*, *Lupinus latifolius*) were more common. Thus, while pothole environments were more benign, they did not alter species composition. Biotic interactions that might affect dominance hierarchies were muted and variable due to wide population fluctuations experienced by *L. lepidus* (Bishop 2002; del Moral & Rozzell 2005). Physical amelioration in potholes promoted more rapid vegetation development so that deterministic processes became prominent. Succession in potholes is a model for how vegetation control may develop across the landscape.

Sources of variation

Changing ordination position of potholes over time shown in DCA suggested succession towards persistent, competitive species (Fig. 5). Turnover was 2 HC along DCA-1 and 1 HC along DCA-2. Variation within years declined along DCA-1, which suggested a reduction of stochastic effects. While only 36% of the species variation was explained, this value is comparable to those found in other studies using either RDA or canonical correspondence analysis (CCA) (e.g. van Oijen et al. 2005; Hasse & Daniëls 2006). More variance can be explained when mature vegetation at larger scales is explored (e.g. Sieben et al. 2009, 43%); explanatory power can be strong when management practices are included (e.g. Jongeman et al. 1987, 63%; Pakeman et al. 2009, 50%); and substantial explanatory power can be achieved using biotic factors (Anthelme et al. 2003, 62%). In contrast, Blatt et al. (2005) offered a cogent analysis of succession with low explained variance. Early in succession on the nearby barren plains of Mount St. Helens (1992), only spatial factors had explanatory value (del Moral et al. 1995, 15%), while more recent landscape studies on Mount St. Helens explained 28 to 35% of the variation (del Moral et al. 2007). Studies that add biological variables or management can therefore improve predictability. In this case, early stochastic effects appear to become muted as environmental and biological filters gain more power.

Development of deterministic control

Many studies have shown that dispersal effects dominate early assembly (Kazmierczak et al. 1995; Endo et al. 2008; Erschbamer et al. 2008; Prach & Hobbs 2008; Rehounkova & Prach 2008), and in less stressful or more mature sites, greater control by deterministic factors is common. Shiels et al. (2008) showed that predictability on landslides was determined by soil factors, even though slides were adjacent to mature vegetation. Hodkinson et al. (2003) found that deterministic factors dominated glacial forelands because the potential flora was small and composed of effective dispersers; similarly, Cannone & Seppelt (2008) were able to classify lichen communities in the desolate interior of Antarctica. Convergence in forests is often driven by competition (Woods 2007).

The succession trajectory described here suggests developing deterministic effects are largely due to increasing effects of local factors: ephemeral species declined, while those with strong vegetative growth and greater longevity increased. In 2008, potholes with similar composition often occurred in scattered sites. In 2001, spatial variation of CTs was lower, which suggested that spatial factors were then influencing composition. Position effects noted through 2001 seem to have been overridden as species composition changed in response to local factors and competition. Even though different methods were used and, before 2001, slightly different sets of potholes were studied, the shift appears real since it is associated with increasing dominance of persistent species. The inter-set correlations increased steadily over time. Biotic influences of dominant species can be expected to affect subordinates, as De Bellis et al. (2007) demonstrated that microfungal communities responded to understorey plants.

The shift from spatial to environmental factors was clarified by covariance analysis. In 1993, 1997 and 2001, only spatial effects were significant, while in 2006 and 2008 those effects were not significant. Soil factors became prominent predictors as species developed in these potholes. By 2008, species were best associated with environmental variables, where structure is being imposed on the vegetation by local factors and a few dominant species. Soil properties should increase their explanatory power (e.g. Dolezal et al. 2008), although erratic invasion of conifers may create alternative communities (Walker & del Moral 2009). As *Lupinus* continues to enhance fertility, pothole vegetation can be expected to become denser, with similar dominance hierarchies developing in most sites.

Limits to convergence

The present study describes community dynamics on pumice at Mount St. Helens from early in species assembly to 2008. For the first time, a shift from stochastic towards deterministic control of succession has been demonstrated directly. A total of 64% of the variation remains unexplained, but overall explained variation associated with local factors has increased. This result should encourage efforts of restorationists seeking to reach defined targets. Greater predictability is likely as vegetation develops and becomes fertile (del Moral et al. 2007): pothole vegetation responded to more effective environmental and biological filters as fertility improved.

Disturbances from elk and further volcanic eruptions continue to enhance heterogeneity and may promote alternative succession trajectories. Ghosts of stochastic processes past will continue to haunt these potholes in the form of persistent priority effects of species such as *Penstemon*, *Luetkea* and *Arctostaphylos* that occupy space, resist invasion and permit different species to dominate environmentally similar potholes. Varying concentrations of *Lupinus* will promote asynchronous development of fertility and therefore promote variable rates of succession. While pothole vegetation may remain heterogeneous, the samples will become more tightly tied to their local environments and overall similarity is likely to increase.

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References

Analytical Software. 2008. *Statistix 9*. Analytical Software, Tallahassee, FL, US.

Anthelme, F., Michalet, R., Barbaro, L. & Brun, J.J. 2003. Environmental and spatial influences of shrub cover (*Alnus viridis* DC.) on vegetation diversity at the upper tree line in the inner western Alps. *Arctic, Antarctic and Alpine Research* 35: 48–55.

Bakker, J.D. & Moore, M.M. 2007. Controls on vegetation structure in Southwestern ponderosa pine forests, 1941 and 2004. *Ecology* 88: 2305–2319.

Battaglia, L.L. & Collins, B.S. 2006. Linking hydroperiod and vegetation response in Carolina bay wetlands. *Plant Ecology* 184: 173–185.

Bischoff, A., Waarthemann, G. & Klotz, S. 2009. Succession of floodplain grasslands following reduction in land use intensity: the importance of environmental conditions, management and dispersal. *Journal of Applied Ecology* 46: 241–249.

Bishop, J.G. 2002. Early primary succession on Mount St. Helens: the impact of insect herbivores on colonizing lupines. *Ecology* 79: 191–202.

Bishop, J.G., Fagan, W.F., Schade, J.D. & Crisafulli, C.M. 2005. Causes and consequences of herbivory on prairie lupine (*Lupinus lepidus*) in early primary succession. In: Dale, V.H., Swanson, F.J. & Crisafulli, C.M. (eds.) *Ecological recovery after the 1980 eruptions of Mount St. Helens*. pp. 151–162. Springer, New York, NY, US.

Blatt, S.E., Crowder, A. & Harmsen, R. 2005. Secondary succession in two southeastern Ontario old-fields. *Plant Ecology* 177: 25–41.

Bossuyt, B., Honnay, O. & Hermy, M. 2003. An island biogeographical view of the successional pathway in wet dune slacks. *Journal of Vegetation Science* 14: 781–788.

Cannone, N. & Seppelt, R. 2008. A preliminary floristic classification of southern and northern Victoria Land vegetation, continental Antarctica. *Antarctic Science* 20: 553–562.

Cutler, N.A., Belyea, L.R. & Dugmore, A.J. 2008. The spatiotemporal dynamics of primary succession. *Journal of Ecology* 96: 231–246.

De Bellis, T., Kernaghan, G. & Widden, P. 2007. Plant community influences on soil microfungal assemblages in boreal mixed-wood forests. *Mycologia* 99: 356–367.

del Moral, R. 1999. Plant succession on pumice at Mount St. Helens, Washington. *American Midland Naturalist* 141: 101–114.

del Moral, R. & Eckert, A.J. 2005. Colonization of volcanic deserts from productive patches. *American Journal of Botany* 92: 27–36.

del Moral, R. & Ellis, E.E. 2004. Gradients in heterogeneity and structure on lahars, Mount St. Helens, Washington, USA. *Plant Ecology* 175: 273–286.

del Moral, R. & Jones, C.C. 2002. Early spatial development of vegetation on pumice at Mount St. Helens. *Plant Ecology* 162: 9–22.

del Moral, R. & Lacher, I.L. 2005. Vegetation patterns 25 years after the eruption of Mount St. Helens, Washington. *American Journal of Botany* 92: 1948–1956.

del Moral, R. & Rozzell, L.R. 2005. Effects of lupines on community structure and species association. *Plant Ecology* 181: 203–215.

del Moral, R., Titus, J.H. & Cook, A.M. 1995. Early primary succession on Mount St. Helens, Washington, USA. *Journal of Vegetation Science* 6: 107–120.

del Moral, R., Wood, D.M. & Titus, J.H. 2005. Proximity, microsites and biotic interactions during early primary succession. In: Dale, V.H., Swanson, F.J. & Crisafulli, C.M. (eds.) *Ecological recovery after the 1980 eruptions of Mount St. Helens*. pp. 93–109. Springer, New York, NY, US.

del Moral, R., Walker, L.R. & Bakker, J.P. 2007. Insights gained from succession for the restoration of landscape structure and function. In: Walker, L.R., Walker, J. & Hobbs, R.J. (eds.) *Linking restoration and succession in theory and in practice*. pp. 19–44. Springer, New York, NY, US.

Dolezal, J., Homma, K., Takahaski, K., Vyatkina, M.P., Yakubov, V., Vetrova, V.P. & Hara, T. 2008. Primary succession following deglaciation at Koryto Glacier Valley, Kamchatka. *Arctic, Antarctic and Alpine Research* 40: 30–322.

Ejrnaes, R., Bruun, H.H. & Graae, B.J. 2006. Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology* 87: 1225–1233.

Endo, M., Yamamura, Y. & Tanaka, A. 2008. Nurse-plant effects of a dwarf shrub on the establishment of tree seedlings in a volcanic desert on Mt, Fuji, central Japan. *Arctic, Antarctic and Alpine Research* 40: 335–342.

Erschbamer, B., Niederfringer Schlag, R. & Winkler, E. 2008. Colonization processes on a central Alpine glacier foreland. *Journal of Vegetation Science* 19: 855–862.

Halvorson, J.J., Smith, J.L. & Kennedy, A.C. 2005. Lupine effects on soil development and function during early primary succession at Mount St. Helens. In: Dale, V.H., Swanson, F.J. & Crisafulli, C.M. (eds.) *Ecological recovery after the 1980 eruptions of Mount St. Helens*. pp. 243–254. Springer, New York, NY, US.

Hasse, T. & Daniëls, F.J.A. 2006. Species responses to experimentally induced habitat changes in a *Corynephorus* grassland. *Journal Vegetation Science* 17: 135–146.

Hodkinson, I.A., Coulson, S.J. & Webb, N.R. 2003. Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. *Journal of Ecology* 91: 651–663.

Hubbell, S.P. 2001. *The unified theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.

Jentsch, A., Friedrich, S., Steinlein, T., Beyschlag, W. & Nezadel, W. 2009. Assessing conservation action for substitution of missing dynamics on former military training areas in Central Europe. *Restoration Ecology* 17: 107–116.

Jongeman, R.H.G., ter Braak, C.J.F. & Van Tongeren, O.F.R. 1987. *Data analysis in community and landscape ecology*. Puduc, Wageningen, NL.

Jumpponen, A., Väre, H., Mattson, K.G., Ohtonen, R. & Trappe, J.M. 1999. Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology* 87: 98–105.

Kazmierczak, E., van der Maarel, E. & Noest, V. 1995. Plant communities in kettle-holes in central Poland: chance occurrence of species? *Journal Vegetation Science* 6: 863–874.

Lepori, F. & Malmqvist, B. 2009. Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos* 118: 471–479.

Lepš, J. & Rejmánek, M. 1991. Convergence or divergence: what should we expect from vegetation succession? *Oikos* 62: 261–264.

Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK.

Lord, J.M., Wilson, J.B., Steel, J.B. & Anderson, B.J. 2000. Community reassembly: a test using limestone grassland in New Zealand. *Ecology Letters* 3: 213–218.

MacDougall, A.S., Wilson, S.D. & Bakker, J.D. 2008. Climatic variability alters the outcome of long-term community assembly. *Journal of Ecology* 96: 346–354.

Mathsoft. 2001. *Axum 7 for Windows*. Insightful Corporation, Seattle, WA, US.

McCune, B. & Allen, T.H.F. 1985. Will similar forests develop on similar sites? *Canadian Journal of Botany* 63: 367–376.

McCune, B. & Mefford, M.J. 2006. *PC-ORD, multivariate analysis of ecological data, version 5.0*. MjM Software Design, Gleneden Beach, OR, US.

National Geographic Society. 2008. *TOPO! 4.5*. National Geographic Maps, Evergreen, CO, US.

Oksanen, J. & Tonteri, T. 1995. Rate of compositional turnover along gradients and total gradient length. *Journal of Vegetation Science* 6: 815–824.

Pakeman, R.J., Lepš, J., Kleyer, M., Lavorel, S. & Garnier, E.the VISTA consortium. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. *Journal of Vegetation Science* 20: 148–159.

Prach, K. & Hobbs, R.J. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology* 16: 363–366.

Prach, K., Pyek, P. & Jaroik, V. 2007. Climate and pH as determinants of vegetation succession in Central European man-made habitats. *Journal of Vegetation Science* 18: 701–745.

Rehounkova, K. & Prach, K. 2008. Spontaneous vegetation succession in gravel-sand pits: a potential for restoration. *Restoration Ecology* 16: 305–312.

Sesnie, S.E., Finegan, B., Gessler, P.E. & Ramos, Z. 2009. Landscape-scale environmental and floristic variation in Costa Rican old-growth rain forest remnants. *Biotropica* 41: 16–26.

Shiels, A.B., West, C.A., Weiss, L., Klawinski, P.D. & Walker, L.R. 2008. Soil factors predict initial plant colonization on Puerto Rican landslides. *Plant Ecology* 195: 165–178.

Sieben, E.J.J., Mucina, L. & Boucher, C. 2009. Scaling hierarchy of factors controlling riparian vegetation patterns of the Fynbos Biome at Western Cape, South Africa. *Journal of Vegetation Science* 20: 17–26.

ter Braak, C.J.F. & Šmilauer, P. 2007. *CANOCO—A FORTRAN program for canonical community ordination (version 4.5)*. DLO-Agricultural Mathematics Group, Wageningen, NL.

Trowbridge, W.B. 2007. The role of stochasticity and priority effects in floodplain restoration. *Ecological Applications* 17: 1312–1324.

van Oijen, D., Hommel, P., den Ouden, J. & de Waal, R. 2005. Effects of tree species composition on within-forest distribution of understorey species. *Applied Vegetation Science* 8: 155–166.

Velazquez, E. & Gomez-Sal, A. 2008. Landslide early succession in a neotropical dry forest. *Plant Ecology* 199: 295–308.

Walker, L.R. & del Moral, R. 2003. *Primary succession and ecosystem rehabilitation*. Cambridge University Press, Cambridge, UK.

Walker, L.R. & del Moral, R. 2009. Transition dynamics in succession: implications for rates, trajectories and restoration. In: Hobbs, R.J. & Suding, K.N. (eds.) *New models for ecosystem dynamics and restoration*. pp. 33–49. Island Press, Washington, DC, US.

Woods, K.D. 2007. Predictability, contingency and convergence in late succession: slow systems and complex data-sets. *Journal of Vegetation Science* 18: 543–554.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species encountered in potholes, 1993 to 2008. Growth forms: DF = deciduous forb; DS = deciduous shrub; DT = deciduous tree; EF = evergreen forb; ES = evergreen shrub; ET = evergreen tree (conifer); G = graminoid; THAL = thallus (mosses). Life forms: Phan-scap = Phanerophyte-scapose, single stem tree, > 5-m tall when mature, canopy above ground; Phan-caesp = Phanerophyte-caespitose, multi-stem shrub, shoots typically > 0.5 m, canopy at ground; Cham = Chamaephyte, woody plants typically < 0.5-m tall, multi-stemmed and often spreading along ground; Hemi = Hemicryptophyte, perennial herb, reduced annually to remnant shoots at or near ground (includes mosses); Geo = Geophyte (cryptophytes), perennial herb, reduced to belowground storage organ during unfavourable period, usually as bulb or rhizome; Ther = Therophyte, annual, these are all forbs, completing their life cycle in a single year.

Appendix S2. Cover of dominant species in the six community types (CT), 2008. Species ordered by DCA. Only species that occurred in at least 30 potholes or had significant patterns are listed. Differences between means in a column were determined by ANOVA, followed by Bonferroni comparisons. DP = degree of persistence: 1 = short-lived; 2 = perennial, compact; 3 = rhizomatous or evergreen; 4 = mosses; 5 = woody, often prostrate.

Appendix S3. Changes in species composition 1993 to 2007. A. Absolute cover of more abundant species; B. Absolute cover of less common species; C. Relative cover of more abundant species; D. Relative cover of less common, rarer species.

Figure S1. Pumice Plain vegetation, 2005.

Figure S2. Pumice Plain and Mount St. Helens, 2005.

Figure S3. Pumice Plain and Loowit Falls, 2005.

Figure S4. Pumice Plain with dense lupines promoting succession, 2007.

Figure S5. Vegetation in dense pothole, 2009; dominated by *Lupinus lepidus*, with *Salix sitchensis* and *Agrostis pallens*.

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