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Long-term effects of *Lupinus lepidus* on vegetation dynamics at Mount St. Helens

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Abstract

The nitrogen-fixing legume *Lupinus lepidus* is the most abundant herb on new volcanic surfaces at Mount St. Helen. We compared vegetation structure in 30 *Lupinus* colonies in three age classes (old, mature, or young based on known years of their establishment) to adjacent sites that were sparsely populated by *Lupinus*. Our goals were to determine if the age of colonies affected either species composition or vegetation structure and if colonies altered vegetation structure of a site. Species richness increased with site age and colonies had significantly greater richness. Mature colonies had lower cover and frequency of other species, while old colonies had significantly higher cover of other species, particularly mosses. Frequencies in colonies were higher than in adjacent sites. Diversity measures were highest in old colonies and least in mature ones. ANOVA showed that density effects of *Lupinus* were stronger than age effects on richness, cover, frequency, dominance, and diversity. The floristic similarity between colonies and adjacent sites declined with colony age, and sites without *Lupinus* became heterogeneous with age. Detrended correspondence analysis demonstrated floristic change as colonies aged and that the differences between colonies and sparse sites increased with age. Regressions of *Lupinus* frequency with measures of structure showed weak second order relationships that suggested that low densities of *Lupinus* inhibited other species, while higher densities promoted abundance and diversity. Together these results suggest that *Lupinus* is a key element that alters floristic successional trajectories and accelerates succession. However, its effects are complicated by the wide ranges of *Lupinus* density, the sequence of invasion, and by herbivores.

Introduction

Plants readily colonize new habitats including glacier forelands (Jumpponen et al. 1998; Jones and del Moral 2005), slack dunes (Berendse et al. 1998), coastal dunes (Olff et al. 1993), and volcanoes (del Moral and Grishin 1999), but infertility often retards succession (Walker et al. 2003). Therefore, species with nitrogen-fixing symbionts may facilitate vegetation. However, the net effects of N-fixers may be positive or negative on particular species (Holmgren et al. 1997; Uliassi and Ruess 2002). Positive effects of N-fixers may include increased moisture, organic matter, physical protection, and seed trapping (Bertness and Callaway 1994). On volcanoes, N-fixing species ameliorate substrates (Vitousek and Walker 1989) and can alter the trajectory and rate of succession (Clarkson and Clarkson 1995). Vascular plants respond individualistically to stresses imposed by infertility, so sites with N-fixers will develop successional trajectories that differ from other sites (Bellingham et al. 2001). Herbivory (Wood and Anderson 1990; Bach 2001), physical amelioration, seed trapping, and competition (Callaway and Walker 1997) can all alter course and rate of primary succession.

Lupinus lepidus Dougl. ex Lindl., the most studied species on new volcanic substrates on Mount St. Helen (Washington state, USA; Tsuyuzaki et al. 1997; Bishop et al. 2005), initially inhibited other species (Wood and Morris 1990). However, *Lupinus* improves soil fertility and ameliorates the physical environment (Braatne and Bliss 1999), potentially producing facilitation (e.g., Fagan et al. 2004). Here, we explore how these opposing tendencies change as *Lupinus* colonies develop. Our objectives are to determine if vegetation structure in *Lupinus* colonies of different ages differs significantly and to determine if floristic contrasts between colonies and adjacent sparse populations change with colony age.

Materials and methods

Study sites and species

All plots were in the blast zone of the 1980 Mount St. Helens eruption, within 3 km of the crater. A plain (approximately 25 km^2) formed when the north side of the cone collapsed causing a landslide. A strong directional blast followed immediately to produce thick deposits of pumice, and pyroclastic flows covered the area below the cone to depths exceeding 40 m (Swanson and Major 2005), resulting in an infertile landscape devoid of vegetation

Lupinus lepidus, a small, poorly dispersed, short-lived wintergreen legume (Bishop and Schemske 1998), was the first plant species recorded in the study area. Exactly where it established within an area was unpredictable from environmental factors, though there were large-scale patterns to colonization. In 1981 small, dense populations were first observed on pyroclastic sites (Bishop et al. 2005). There were no obvious habitat differences between colonies and adjacent barren sites (Wood and Morris 1990). These "old" populations, established between 1981 and 1984, were invaded by other species, but were still distinct in 2003. They have experienced four cycles of high abundance followed by a population crash associated with herbivory (Bishop et al. 2005). From the late 1980s to the mid-1990s, *Lupinus* formed dense colonies as populations of typical pioneer species were also becoming established (del Moral et al. 1995). These "mature" colonies were 12–15 years old when sampled. In some areas, intense herbivory on *Lupinus* may have delayed the development of colonies (Bishop 2002), while in higher-elevation sites, dispersal limitations and environmental stresses slowed development (Lawrence 2005). We also sampled "young" colonies that began to develop in 1999 (Bishop et al. 2005), after other species had established. These colonies were no more than four years old when sampled.

The study was conducted during 2001-3. The sampled sites were near their peak of *Lupinus* abundance in each year. Each site included a dense *Lupinus* colony and a "sparse site," an adjacent area of vegetation where *Lupinus* individuals were scattered, but vegetation cover was modest. Ten old sites, centered at 1130 ± 40 m (46°14′34″ N; 122°10′02″ W), were sampled on pyroclastic materials. To the east, 13 mature sites on pumice were centered near 1270 ± 15 m (46°13′51″ N; 122°09′37″ W). Seven young sites were sampled above 1340 ± 17 m (46°13′31″ N; 122°09′48″ W) on pumice. Colonies and sparse populations of *Lupinus* occurred on similar, homogeneous substrates. We believe that stochastic processes permitted the localized establishment of *Lupinus* colonies, though subtle site differences remain a possibility to be tested experimentally. The vegetation near colonies varied, but included grasses (e.g., *Agrostis pallens* Trin and *A. scabra* Willd.), sedges (e.g., *Carex mertensii* Prescott ex Bong.), wind-dispersed species (e.g., *Anaphalis margaritacea* (L.) B. & H., *Chamerion angustifolium* (L.) Holub, and *Hypochaeris radicata* L.) and herbs tolerant of barren sites (e.g., *Juncus parryi* Engelm and *Cistanthe umbellata* (Torr.) Hershkovitz). Nomenclature follows the Integrated Taxonomic Information System (http://www.itis.usda.gov/advanced_search.html).

Sampling

The *Lupinus* colonies and sparse sites were each sampled with 20 noncontiguous 1-m^2 quadrats that alternated along a 20 m transect. Spatial auto-correlation among the quadrats was thus minimized, while the colonies and sparse samples were sufficiently close (within 15 m and nearly parallel) to be compared directly. To facilitate estimates of abundance, each quadrat was divided into 25 400-cm^2 sub-quadrats. Cover of vascular plants and mosses within each sub-quadrat was estimated. Frequency based on 500 sub-quadrats per transect was used as a more reliable estimate of abundance of graminoids.

Analyses

There were six sets of transects divided into three age classes (old, mature = intermediate age, young) and two density classes (colony and sparse). Mean richness per quadrat and total richness per transect were determined. Transect mean cover and frequencies of each species were calculated. The Shannon-Wiener diversity index (H′) and the complement of Simpson's index (dominance, D) were calculated from frequency (McCune and Mefford 1999). Because we were interested in how *Lupinus* altered structure, we also calculated H′ and D after excluding *Lupinus*. Mosses were often common, possibly obscuring subtle signals in the vascular plant community. Therefore, we calculated structural indices after excluding mosses. Transect means were analyzed by one-way ANOVA. Analysis at the quadrat level used a mixed-model ANOVA with age and density nested within age as fixed effects and transects treated as a random variable. We used *Lupinus* frequencies in linear regressions to predict measures of vegetation structure at the quadrat level.

The mean percent similarity (PS) of quadrats within each transect was calculated from the species frequency of all possible quadrat pairs in order to determine internal heterogeneity. PS among transects of each age-density combination was calculated to explore changing patterns of heterogeneity. The PS between dense and sparse transects of each site was calculated to determine the degree to which *Lupinus* altered species composition (Kovach 1999):

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

where x is the frequency of species k in samples i and j.

Compositional changes in transects were explored using DCA (McCune and Mefford 1999) after excluding species with < 4 occurrences. Axes were scaled in half-changes, so that differences in the axis scores reflect floristic differences between transects. Several analyses were conducted: all species, exclusion of *Lupinus*, and exclusion of *Lupinus* and mosses.

Results

Community composition

We investigated the contrasting effects of dense and sparse *Lupinus* populations and of their different approximate ages on species composition and vegetation structure in several ways.

Species composition
There were 57 species in this study, but only 31 occur in more than three of the 60 transects. The most abundant species was *Lupinus lepidus*. In sparse sites its frequency was typically less than half that of colonies, with a minimum occurring next to mature colonies (Figure 1). *Agrostis pallens* frequency declined with the age of *Lupinus* colonies, but it was higher in young and mature colonies than in the respective sparse sites. *A. scabra* was variable, and colonies and sparse sites were similar. The introduced species *Hypochaeris radicata* was infrequent except in old colonies, while

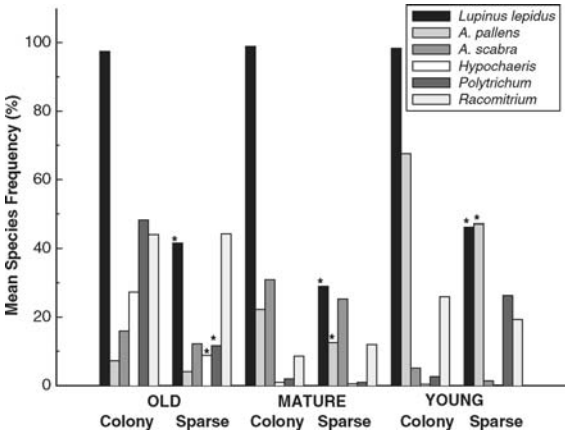

Figure 1. Mean frequency of representative species in the six transect types. * = frequencies that differ between colonies and sparse sites ($p < 0.05$, paired t-test). *A. pallens* = *Agrostis pallens*; *A. scabra* = *Agrostis scabra*; *Hypochaeris* = *H. radicata*; *Polytrichum* = *P. juniperinum*; *Racomitrium* = *R. canescens*.

the moss *Polytrichum juniperinum* Hedw. was frequently found growing with *Lupinus*. In young and mature habitats, the moss *Racomitrium canescens* (Hedw.) Brid. had (non-significantly) higher frequencies in colonies than in sparse sites. Other species, including *Carex mertensii*, *Cistanthe umbellata*, *Juncus parryi*, and *Penstemon cardwellii* Howell, were widely distributed at moderate frequency. These species showed no pronounced trends with either age or density.

Species richness

Colonies had 27, 46, and 41 species in young, mature, and old sites, while adjacent sparse sites had 21, 32, and 38 species, respectively. Colonies always contained more species than did sparse ones, but paired *t*-tests were not significant. Mean species richness per transect increased with age and with *Lupinus* density (Table 1). Density effects within age classes were much stronger than age effects (Table 2). Eliminating mosses reduced the strength of both effects, suggesting that mosses contributed to much of the variation in mean richness.

Percent cover

When *Lupinus* was included, cover was, of course, much higher in colonies than in sparse sites (Table 1) and total cover also increased from young to old colonies. The exclusion of *Lupinus* revealed that percent cover of other species was also higher in colonies than in sparse sites, though the difference was least in mature colonies. The cover of sparse old sites was significantly higher than that of the young sparse sites. When mosses were excluded, the cover contrasts between colonies and sparse sites remained, but cover among colonies and among sparse sites was similar. Mosses appear to require the establishment of some vascular plants before they can become common, and are benefited by *Lupinus*. The effects of *Lupinus* on cover were stronger than the effects of age if mosses are included. When mosses were eliminated, the effect of age disappears. Thus, mosses appear to be the primary taxa that respond positively to *Lupinus* (Table 2).

Frequency, dominance, and diversity

Frequency (%), Simpson dominance (D), and diversity (H′) revealed significant patterns (Figures 2–4). In each figure, the three groups of data are based on all species, excluding *Lupinus*, and excluding *Lupinus* and mosses.

Lupinus colonies had higher frequency than did the adjacent sparse sites, even when *Lupinus* and mosses were excluded. Frequency in colonies and sparse sites was highest in old sites, but least in mature ones (Figure 2). Excluding *Lupinus* revealed comparable patterns. Old, sparse sites had higher frequencies than did other sparse sites, while mature colonies had the lowest frequency among colonies. However, when mosses were excluded, there were no differences among either colonies or sparse sites of different ages. The nested analysis showed a high degree of variation, with the density effect dominating the effect of age

Table 1. Mean richness and percent cover in *Lupinus* colonies and in sparsely populated sites, in three age classes (old, mature and young).

Parameter	Old, colony	Old, sparse	$p<$	Mature, colony	Mature, sparse	$p<$	Young, colony	Young, sparse	$p<$
Mean Richness									
Transect-Mean	16.6^{a}	14.7^{ab}	0.08	15.7^{ab}	14.4^{ab}	0.09	13.0^{ab}	10.9^{b}	0.09
SD	3.2	1.8		2.8	2.6		1.6	3.8	
Quadrat	6.9^{a}	5.5^{b}	0.001	5.1^{c}	4.9^{c}	NS	4.5^{c}	3.6^{d}	0.05
SD	1.88	1.95		2.03	1.91		1.72	1.86	
Mean Percent Cover									
All species	115.0^{a}	52.7^{c}	0.0001	102.5^{ab}	33.9^{c}	0.0001	91.0^{b}	37.6^{c}	0.001
SD	24.3	14.6		17.1	9.3		15.3	8.7	
Excluding lupine	61.5^{a}	39.3^{b}	0.02	30.6^{bc}	22.7^{c}	0.05	41.3^{b}	23.2^{bc}	0.05
SD	19.5	13.2		8.0	7.0		18.5	8.3	
No lupine or moss	30.7^{ab}	20.3^{ab}	0.02	26.2^{ab}	19.7^{b}	0.004	33.7^{a}	18.1^{b}	0.03
SD	16.3	10.1		5.9	3.4		13.1	9.1	

SD = standard deviation of the means. Pairs that differ significantly (paired *t*-test of transect means) indicated after "sparse" entry. Superscripts in a row indicate homogeneous groups determined by ANOVA, followed by Bonferroni tests ($p < 0.05$).

Table 2. Summary of nested analyses of variance.

Basis	Parameter	Source of Variation	*F*-value	*p*-value
All Species	Richness	Intercept	807.5	0.000
		Density (Age)	35.0	0.000
		Age	8.5	0.001
Lupinus	Richness	Intercept	600.1	0.000
		Density (Age)	30.6	0.000
		Age	9.8	0.001
Lupinus, Mosses	Richness	Intercept	492.2	0.000
		Density (Age)	15.1	0.000
		Age	4.0	0.031
All Species	Cover	Intercept	1762.4	0.000
		Density (Age)	917.3	0.000
		Age	12.4	0.000
Lupinus	Cover	Intercept	556.1	0.000
		Density (Age)	117.1	0.000
		Age	23.9	0.001
Lupinus, Mosses	Cover	Intercept	253.1	0.000
		Density (Age)	94.9	0.000
		Age	0.4	0.681
All Species	Frequency	Intercept	1244.2	0.000
		Density (Age)	316.9	0.000
		Age	24.9	0.000
Lupinus	Frequency	Intercept	595.5	0.000
		Density (Age)	96.0	0.000
		Age	24.3	0.000
Lupinus, Mosses	Frequency	Intercept	285.6	0.000
		Density (Age)	67.1	0.000
		Age	0.5	0.603
All Species	Dominance	Intercept	4210.7	0.000
		Density (Age)	26.3	0.000
		Age	9.3	0.001
Lupinus	Dominance	Intercept	539.3.1	0.000
		Density (Age)	20.1	0.000
		Age	2.8	0.079
Lupinus, Mosses	Dominance	Intercept	425.4	0.000
		Density (Age)	8.2	0.000
		Age	4.2	0.026
All Species	Diversity	Intercept	1489.4	0.000
		Density (Age)	24.7	0.000
		Age	8.4	0.001
Lupinus	Diversity	Intercept	436.8	0.000
		Density (Age)	22.0	0.000
		Age	4.2	0.026
Lupinus, Mosses	Diversity	Intercept	350.2	0.000
		Density (Age)	8.2	0.000
		Age	4.4	0.022

The fixed effects are density (2 levels) within age and age (3 levels); the 60 transects form a random variable. *Lupinus*: calculations after *Lupinus* was excluded from the data; *Lupinus*, mosses: calculations after *Lupinus*, *Racomitrium*, and *Polytrichum* were excluded.

(Table 2). When mosses were also excluded, the density effect remained, but there was no effect of age. Again, it appears that positive effects of *Lupinus* were due primarily to the response of mosses. D-values of colonies and sparse sites were similar, but with exceptions (Figure 3). With all species, or with *Lupinus* and mosses excluded, mature sparse sites had higher D-values than did mature colonies. D-values increased with age, significantly so among the sparse sites. Nested analyses revealed the large variation among sites, and the significant effect of density on dominance. Dominance varied with age, except when *Lupinus* was excluded, but the effect was small (Table 2).

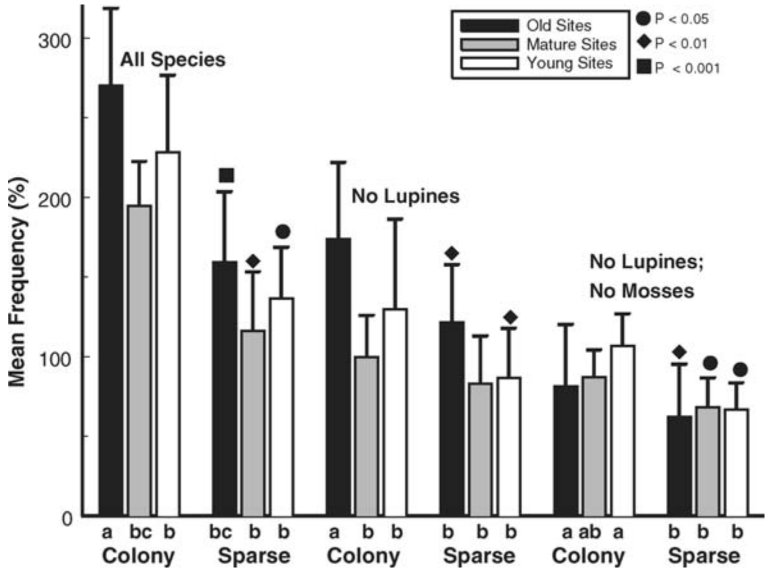

Figure 2. Mean species frequency (%) in *Lupinus* colonies and adjacent sparse sites, calculated from all species and after excluding *Lupinus*, and after excluding *Lupinus* and the mosses *Racomitrium* and *Polytrichum* from the calculations. Symbols indicate differences between *Lupinus* colonies and sparse sites (paired *t*-tests), while ANOVA indicates strength of overall differences among the six samples of a set.

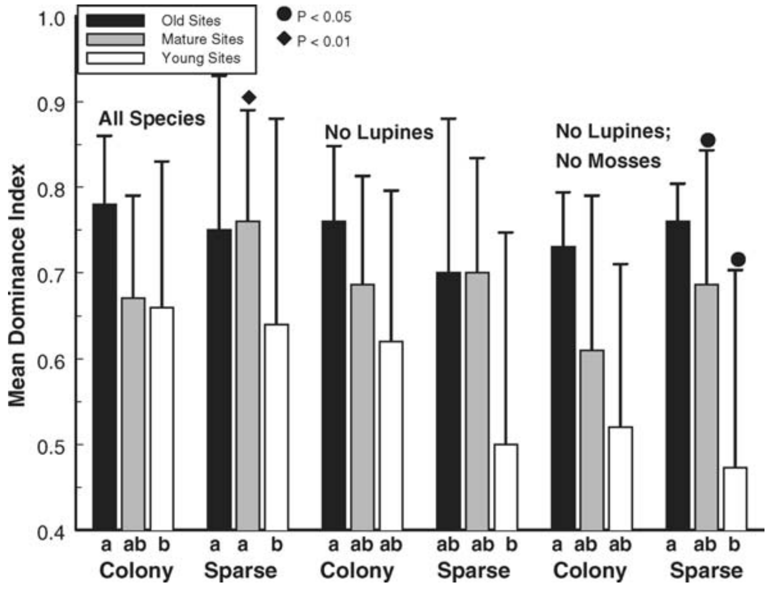

Figure 3. Dominance index (D) in *Lupinus* colonies and adjacent sparse sites, calculated from all species and after excluding *Lupinus*, and after excluding *Lupinus* and the mosses *Racomitrium* and *Polytrichum* from the calculations. Symbols indicate differences between *Lupinus* colonies and sparse sites (paired *t*-tests), while ANOVA indicates strength of overall differences among the six samples of a set.

H′ increased with age when *Lupinus* was included (Figure 4). In mature sparse sites, H′ was higher than in young sites and was greater than in the adjacent *Lupinus* colony. Excluding *Lupinus* produced H′ values that were similar. Young colonies were significantly more diverse than were

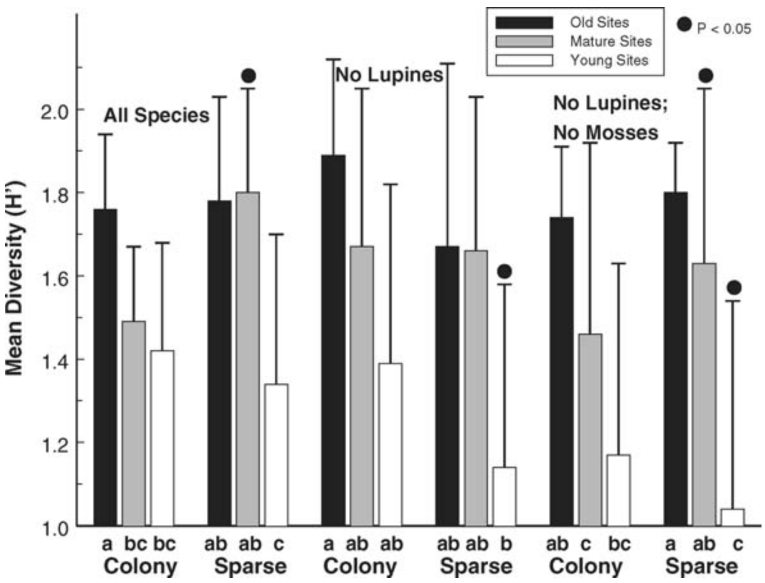

Figure 4. Diversity (H′) in *Lupinus* colonies and adjacent sparse sites, calculated from all species and after excluding *Lupinus*, and after excluding *Lupinus* and the mosses *Racomitrium* and *Polytrichum* from the calculations. Symbols indicate differences between *Lupinus* colonies and sparse sites (paired *t*-tests), while ANOVA indicates strength of overall differences among the six samples of a set.

young sparse sites. When mosses were also excluded, diversity increased with age in both colonies and sparse sites. Mature and old sparse sites were each more diverse than were mature and old colonies. The nested analysis was similar to that for dominance. Age effects were small, though significant, and sites appeared to vary substantially for reasons unrelated to either age or *Lupinus* density. When mosses were excluded, the effects on remaining species were small (Table 2).

Floristic similarity

Percent similarity was calculated within each habitat type based on the individual quadrats. Colonies were more homogeneous than their companion sparse sites when *Lupinus* was included (Table 3). When *Lupinus* was excluded, a strong distinction was retained in old sites, but only an insignificant tendency towards greater homogeneity in colonies was retained. Comparisons among the sparse sites suggested that older ones had differentiated to a greater degree and were therefore less internally more heterogeneous.

The paired PS comparison between colonies and sparse sites across ages was similar with and without *Lupinus* (Table 4). In both cases, young sites were more similar than were mature and old sites.

Lupinus *effects on structure*

The relationships of *Lupinus* frequency (independent variable) to richness, frequency of other species, dominance (D), and diversity (H′) were investigated by linear regression. Second order regression analyses were conducted with transect means. The net frequency predicted by *Lupinus* frequency with all transects showed significant the second order relationship ($r^2 = 0.17$, $p < 0.006$) that was negative at lower *Lupinus* frequencies and positive at higher ones. When mosses were excluded, the relationship was similar ($r^2 = 0.13$, $p < 0.02$). When sparse transects were analyzed after excluding mosses, there was a stronger relationship ($r^2 = 0.28$, $p < 0.02$), but in contrast to the overall data, frequency of other species increased at low to moderate *Lupinus* frequency, and was reduced at higher *Lupinus* frequency.

Analyses were also conducted at the 1-m^2 quadrat level, with and without mosses, to assess the relationships between *Lupinus* and other species. Underlying environmental differences are unlikely to be responsible for different *Lupinus* frequencies since there is very low correlation between such soil factors as moisture content and organic matter (R. del Moral, unpubl. data; J.H. Titus, pers. comm.). Quadrats in colonies and

Table 3. Percent similarity (PS) among transects in each combination of age and density.

Site	Quadrats		Transects	
	All species	*Lupinus* excluded	All species	*Lupinus* excluded
Old colony	75.4 ± 5.84^{ab}	66.8 ± 8.34^{a}	66.2 ± 9.0^{ab}	50.1 ± 12.7^{ab}
Old sparse	*62.3 ± 9.89^{cd}	*55.5 ± 10.2^{ab}	*47.2 ± 16.2^{c}	*36.3 ± 19.7^{c}
Mature colony	75.4 ± 7.3^{ab}	54.7 ± 9.8^{ab}	69.1 ± 10.6^{ab}	44.5 ± 16.2^{abc}
Mature sparse	*52.6 ± 9.9^{d}	49.3 ± 11.6^{b}	*51.8 ± 12.9^{c}	41.3 ± 16.7^{bc}
Young colony	83.9 ± 5.47^{a}	66.9 ± 16.3^{a}	73.3 ± 9.2^{a}	52.4 ± 16.8^{ab}
Young sparse	*67.8 ± 6.0^{bc}	62.0 ± 8.8^{ab}	*61.2 ± 13.2^{b}	54.3 ± 15.8^{a}

Quadrat data are the means from within transects. Superscripts indicate homogeneous groups (ANOVA, then Bonferroni tests; $p < 0.05$). An * indicates sparse sites that differ from the adjacent (dense) colony (paired *t*-test, $p < 0.05$.

Table 4. Percent similarity (PS) between colonies and their adjacent sparely populated sites. Superscripts indicate homogeneous groups (ANOVA, then Bonferroni tests; $p < 0.05$).

Colony vs. sparse	All species	*Lupinus* excluded
Old	47.6 ± 13.1^{b}	40.5 ± 19.4^{b}
Mature	46.7 ± 11.0^{b}	43.7 ± 16.2^{b}
Young	59.2 ± 7.2^{a}	53.4 ± 10.8^{a}

sparse sites were analyzed together, and sparse sites were analyzed separately because the range of *Lupinus* frequencies was larger than that of colonies. In each case, old, mature, and young sites were analyzed separately.

The strongest relationships were with frequency of all other species, though the explained variance, r^2, was low (Table 5). Richness, D, and H' were weakly related to *Lupinus* frequency, and each case, the second order linear regression was significant. Typical results were that *Lupinus* effects were slightly negative at lower frequencies, but positive at higher frequencies. Excluding mosses did not alter this pattern, though the relationship intensified. When only the sparse quadrats were considered, the relationships were weaker.

When quadrats were stratified by age, there were significant, positive relationships among *Lupinus* frequency and all measures of structure in old and young patches. In mature sites, there was only a very weak relationship. Excluding mosses had little effect on these patterns.

When only sparse sites were analyzed by age, relationships were weak. Old, sparse sites had a quadratic pattern for each measure, but there were no significant relationships at mature sites. The pattern in young sites was stronger than the old sites. Excluding mosses weakened most relationships. Many factors influence the structure of associated vegetation in these samples, but the concentration of *Lupinus* is significant.

Detrended correspondence analysis (DCA)

Frequency data were analyzed with DCA to explore compositional changes with age and differences between colonies and sparse sites. These scores, in which 100 units reflect one floristic half-change, were analyzed by ANOVA, followed by the Bonferroni comparison of means. The mean DCA scores changed significantly with age on both axes with and without *Lupinus*. There was a trend from old to young sites on both axes, with old sites different from the others on both axes ($p < 0.01$). Old colonies were significantly different from their sparse companions on DCA-1 and mature colonies differed from mature sparse sites on DCA-2. The DCA scores of age classes determined after excluding *Lupinus* also differed sharply, but colonies and sparse sites of each age were similar in species composition (Figure 5). Young colonies differed from old and mature colonies on DCA-1 ($p < 0.01$), and mature colonies differed from both old and young colonies ($p < 0.01$) on DCA-2. Sparse sites reflected these trends. Scores of young sites differed from old and mature sites ($p < 0.001$) on DCA-1, while scores of mature sites differed from old and young sites ($p < 0.01$) on DCA-2. These differences suggested that sites have developed along successional trajectories to different degrees.

Table 5. Regression of *Lupinus* frequency vs. vegetation structure based on frequency excluding *Lupinus*.

Sample	Richness		Net frequency		Dominance		H′	
	r^2	$p <$	r^2	$p <$	r^2	$p <$	r^2	$p <$
All quadrats	∪0.03	0.0000	∪0.09	0.0000	∪0.02	0.0003	∪0.02	0.0001
Old	0.22	0.0000	∪0.25	0.0000	0.07	0.0000	0.09	0.0000
Mature	NS		0.014	0.007	NS		NS	
Young	∪0.11	0.000	∪0.22	0.0000	∪0.10	0.0000	∪0.09	0.0000
All, no mosses	∪0.04	0.0000	∪0.11	0.0000	∪0.02	0.0001	∪0.02	0.0000
Old	∪0.15	0.0000	∪0.26	0.0000	0.07	0.0000	∪0.09	0.0000
Mature	NS		0.04	0.0000	NS		NS	
Young	∪0.13	0.0000	∪0.22	0.0000	∪0.11	0.0000	∪0.06	0.0000
Sparse quadrats	NS		0.02	0.003	∪0.01	0.05	NS	
Old	∪0.08	0.0003	∪0.11	0.0000	∪0.04	0.02	0.05	0.005
Mature	NS		NS		NS		NS	
Young	∪0.12	0.0002	∪0.23	0.0000	∪0.09	0.0014	∪0.10	0.0006
Sparse, no mosses	∪0.01	0.03	∪0.03	0.0001	NS		NS	
Old	∪0.06	0.0006	∪0.04	0.006	NS		∪0.03	0.02
Mature	NS		0.04	0.003	NS		NS	
Young	NS		0.03	0.05	NS		NS	

All: 1200 quadrats; Sparse: 598 quadrats. "No mosses" indicates regressions based on measures calculated after excluding mosses. (NS: not significant; ∪: indicates second order relationships in which parameter declines at low *Lupinus* frequency, then increases at higher values; other r^2 terms indicate linear first order regressions).

Discussion

Positive and negative effects

Positive effects associated with *Lupinus* are likely due to improved fertility (Halvorson and Smith 1995; Halvorson et al. 2005) and reduced water stress. Other positive effects may result from seed trapping, soil stabilization, and protection from herbivory. Where positive effects dominate, biomass can accumulate more rapidly, and it becomes more likely that species common in latter stages of succession can establish. *Lupinus* mediates other processes. Negative effects are primarily due to competition, but may also result from indirect effects (cf. Levine 1999; Pages and Michalet 2003). For example, *Lupinus* may promote mosses by protecting them from desiccation, leading in turn to less seedling establishment by other species. These *Lupinus* effects also interact with herbivory (Bishop et al. 2005). Other species within old *Lupinus* colonies may suffer disproportionate grazing from elk and grasshopper populations. Such differential grazing, to which mosses are largely immune, could explain the positive effects on mosses noted in old colonies, but not elsewhere. The balance of *Lupinus* effects on community composition appears to change over time. Patterns in mature colonies suggested weak net negative effects, while weak positive relationships were suggested elsewhere. In sparse sites, reduced *Lupinus* density or greater recruitment from adjacent colonies appeared to promote developing vegetation as *Lupinus* populations aged.

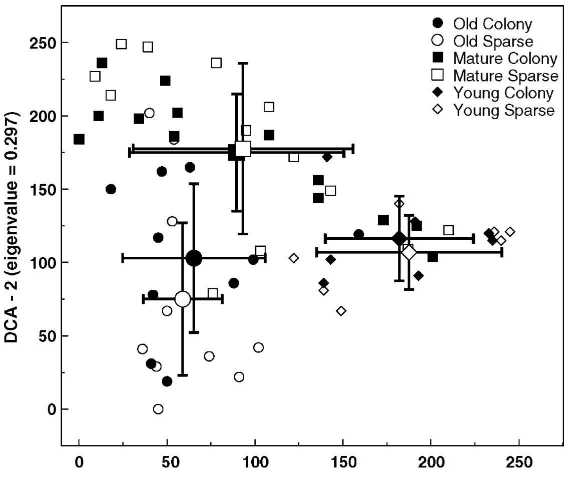

Figure 5. Distribution of 60 transects determined by DCA, excluding *Lupinus*. Axes scaled in units of floristic half-changes (100×). Filled symbols are lupine colonies while open symbols are adjacent sparse sites. Means (± SD.) of each transect type are plotted to emphasize transect differences.

Most dominant plants alter their immediate environment to affect some species positively and others negatively (Uesada and Tsuyuzaki 2004). *Coriaria arborea* facilitated tree species on Mt. Tarawera, New Zealand (Walker et al. 2003), though it inhibited herbs species and its own seedlings. Such effects can change through the lifetime of the dominant (Shumway 2000). The net effects of these mechanisms are often lumped, so that a species is said to facilitate or inhibit the development of the community. It is more accurate to recognize a gradation of effects, from strongly positive to strongly negative, of a dominant on several coexisting and potential successor species. Bellingham et al. (2001) demonstrated that the nitrogen-fixing shrub *Carmichaelia odorata* facilitated several tree species to different degrees, thus altering the trajectory of succession.

Here, the overall effects of *Lupinus* are to enhance the rate of development and to alter the course of succession. Patterns in mature colonies suggested weak net negative effects, while weak positive relationships were suggested in other colonies. However, focusing on net effects may obscure conflicting mechanisms (Wood and del Moral 1987). As colonies age, species such as *Hypochaeris radicata* respond positively to conditions produced by *Lupinus*. This species often invaded where *Lupinus* died. Mosses and *Agrostis scabra* developed well in older *Lupinus* colonies, while other species declined with colony age (e.g., *A. pallens*). Even young colonies produced positive effects on some species. Several early experiments showed that *Lupinus* promoted pioneers (Morris and Wood 1989).

Old colonies were more open than mature ones and species tolerant of *Lupinus* had invaded. We have observed old *Lupinus* patches going through several population cycles (see also Bishop et al. 2005). The fertility and the mulching effects of *Lupinus* litter are more conducive to growth than are dense stands of living plants (Wood and Morris 1990; Halvorson et al. 2005). Young colonies may promote some species because *Lupinus* cannot suppress established plants, which can use the nitrogen leaking from the *Lupinus* rhizosphere. Mature colonies comprise vigorous populations of *Lupinus* that have developed together with other species. Many of these associates have not yet utilized enhanced fertility to compete better with *Lupinus*. We predict that these mature colonies will develop higher densities of mosses, *Hypochaeris*, and *A. scabra*, and that peak *Lupinus* abundance will decline.

We expected that positive effects of *Lupinus* would increase with colony age and that there could be a nonlinear relationship between *Lupinus* frequency and other measures of structure. Though the data were variable, and many other factors mediate species abundance, these expectations were realized. Intermediate frequencies of *Lupinus* reduced richness, frequency, and diversity indices. At higher frequencies of *Lupinus*, positive effects due to wind reduction, temperature amelioration, and fertility enhancements appear to overcome negative effects. The effects when only quadrats from sparse transects were analyzed were weaker, suggesting that *Lupinus* effects differed in the three age classes. When these data were stratified by age, mature sites showed little effect, while other sites showed relatively strong pattern. With mosses excluded, there was a positive linear effect on frequency, but no other factor responded. The response in old colonies was nearly linear and positive, while young colonies had nonlinear responses.

Lupinus was common in most sparse sites. Old and young sparse sites produced nonlinear responses by measures of structure, suggesting that positive effects of *Lupinus* require higher frequencies. The mixed ANOVA indicated that the abundance of *Lupinus* had a greater impact than did the age of the *Lupinus* colony.

Species richness increased with colony age and the frequency of most species was greater within colonies than in sparse sites despite the abundance of *Lupinus*. The effects of *Lupinus* on plant cover were complex. Colonies had higher cover of other species than did the sparse sites, but cover in mature colonies was lower than that of young and old colonies, hinting at inhibition. The greater cover of other species in older colonies was due largely to mosses. Old and young colonies had higher frequency than did adjacent sparse sites, while mature colonies did not. Mosses are often considered essential to early primary succession (Delgadillo and Cárdenas 1995; Poli Marchese and Grillo 2000), but there is no evidence for positive effects.

Diversity indices suggested that mature colonies produced stronger competitive effects than did other colonies, since both dominance (D) and H′ were minimal. When mosses were excluded from calculations, diversity was reduced in old colonies compared to sparse sites, confirming the dominance of mosses in the older colonies.

Trajectories

Many factors govern a vegetation trajectory. While the degree of predictability in primary succession is low due to landscape or priority effects, secondary disturbances, and chance, general predictability (e.g., of functional traits) may be enhanced if the effects of key species are understood (Turner et al. 1997). Plant-mediated change in soil nitrogen is a major way by which plants can alter succession (Maron and Jeffries 1999; Adema et al. 2005).

This study suggests that *Lupinus* alters trajectories within colonies and perhaps also in adjacent, sparsely colonized sites. The trajectories of colonies differed from those of sparse sites due to *Lupinus*, and increased with age, since similarities between colonies and sparse sites declined with age. As soils improve, vegetation development within colonies should exceed that of sparse sites. *Lupinus* colonies also appear to promote those species that can thrive where conditions are ameliorated. These species include the nutrient responsive species *Hypochaeris* and *Polytrichum* (Titus and del Moral 1998). Colonies limit opportunities for others species, including conifers. Floristic variation within *Lupinus* colonies was lower, suggesting that the environment was more homogeneous, while vegetation in sparse sites was more variable, implying greater habitat heterogeneity. Old sparse sites remained dominated by the pioneer species *Penstemon*, *Elymus elymoides* (Raf.) Swetzy, and *Cistanthe* with early pioneers such as *Anaphalis*, *Chamerion*, and *Hieracium* persisting at lower abundances.

Lupinus may mediate the development of a vegetation mosaic in two ways. When they established before other species, *Lupinus* formed dense monocultures that now support mosses and species that respond to higher fertility or that can tolerate negative effects. Invasion of old colonies was facilitated by *Lupinus* population crashes due to herbivory (Bishop 2002) and to its intrinsic population processes. Subsequent *Lupinus* recovery fails to suppress newly arrived invaders, and may enhance their growth.

When *Lupinus* invades existing vegetation, it may enhance other species growth through nitrogen production. If it achieves high densities, it may inhibit some associates, potentially altering trajectories. The contrast between *Lupinus* colonies and adjacent sparse sites provides another way to promote a vegetation mosaic. Sparsely vegetated sites with modest levels of *Lupinus* permit a different set of species to persist (see below).

DCA revealed larger floristic contrasts with age than with *Lupinus* density. This contrasts with the effects on vegetation structure, in which density effects predominated. Density altered the mean ordination scores significantly only between old colonies and old sparse sites. The persistence of *Lupinus* appears to alter the rules for survival. In old colonies, species had to invade occupied, more fertile habitats, while establishment in barrens was constrained by abiotic factors. Different species are successful in these disparate tasks. The continued presence of *Lupinus* causes vegetation to diverge from the adjacent site. Old sparse sites were also more variable than young ones. This suggests that *Lupinus* colonies enhanced floristic heterogeneity in sparse sites by seed dispersal (cf. del Moral and Eckert 2005). Thus, *Lupinus* alone may nudge vegetation development along alternative trajectories both where it is dense and in adjacent sites (cf. Walker and Vitousek 1991). An alternative explanation for differences between colonies and sparse sites is that *Lupinus* colonies established where abiotic conditions were more favorable. However, the pattern of shifting effects (positive in young colonies, negative in mature ones, and then again positive in older colonies) weighs against this possibility, as does the absence of clear physical differences between colony sites and sparse sites.

Lupinus lepidus appears to facilitate succession by accelerating the growth of other species, by enhancing the seed bank of invading species (cf. Clarkson et al. 2002), by reducing seedling mortality, by promoting species found later in succession, and by mediating herbivory, but the pattern is complex. *Lupinus* colonies attract many invertebrate herbivores, some of which also feed on other species. The effect varies geographically and with colony age (cf. Bishop et al. 2005). There is no evidence that *Lupinus* will eventually dominate all sites because it is constrained by poor growth in severe sites, competition in moist sites, shade, and herbivory. Its differential occupancy for several decades should affect the subsequent composition of the understory. Conifers, the pre-eruption dominants, are uncommon, but they eventually should establish, leading to further inhibition and facilitation. The ground layer vegetation will be transformed, with *Lupinus* restricted to margins and gaps. If this proves true, it would be evidence for altered trajectories (Belyea and Lancaster 1999) within one habitat. Unlike the model of Petraitis and Latham (1999), alternative stable states would not depend on broad, differential disturbance events, but rather on different impacts on resource availability.

We determined that as the colony ages, the associated vegetation becomes structurally more complex, richer in species, and more abundant. We also determined that while colonies and sparse sites remain floristically similar, they are less so in old sites. However, the mechanisms by which *Lupinus lepidus* influence primary succession, even in this simple environment, are complex. In addition to the density and age of *Lupinus* populations, the trajectory of primary succession is influenced by herbivory, dispersal, and stochastic events all superimposed on spatial and environmental gradients. The present study suggests directions for experiments to explore interactions of *Lupinus lepidus* with its associates that will clarify our understanding of the vegetation dynamics.

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