Lupine Colonies **(not yet published; shorter version)**

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

by Roger del Moral & Lara Rozzell

Abstract: The nitrogen-fixing legume *Lupinus lepidus* is the most abundant herb on recently formed 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 promoted richness. Mature colonies had lower cover and frequency of other species, while old colonies promoted other species, particularly mosses. Frequencies in colonies were higher than in adjacent sites. Diversity measures were highest in old colonies, least in mature ones. Nested ANOVA showed that the density effects of *Lupinus* were stronger than its age effects. The floristic similarity between colonies and adjacent sites declined with colony age, while sparse sites 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. Linear regressions of *Lupinus* frequency with measures of structure showed weak second order relationships that suggested that low density of *Lupinus* inhibited other species, while higher densities promoted abundance and diversity. Together, these results suggest that *Lupinus* alters floristic successional trajectories, promotes successional development, and affects adjacent vegetation. However, these effects are complicated the wide fluctuations inherent in *Lupinus*, the sequence of invasion, and by herbivores. *Lupinus* remains the key element among several which promote the development of a vegetation mosaic. *Lupinus* will continue to affect future vegetation long after conifers exclude it due to its effects on soil.

LUPINE COLONIES are dense sites dominated by *Lupinus lepidus*, the most studied species on Mount St. Helens. Some patches were established in 1981, others only within the last few years. Between 2001 and 2003, we sampled 30 patches and found interesting contrasts between young, mature and old patches. In each patch, a belt of 20 alternatiing1-m^2 quadrats was established. A comparable transect was established outside the patch parallel to the first one. Species cover and frequency were determined for each quadrat based on 25 sub-quadrats. Data are reported for frequency, which does not give undue weight to less abundant species. 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.

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* (of course). In sparse sites its frequency was typically less than half that of colonies, with a minimum occurring next to mature colonies (Fig. 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 the moss *Polytrichum juniperinum* Hedw. also benefited by 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). The nested analysis showed that density effects within age classes were much stronger than age effects (Table 2; showing only results excluding lupines and excluding lupines and mosses). Eliminating mosses reduced the strength of both effects, suggesting that mosses contributed too 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).

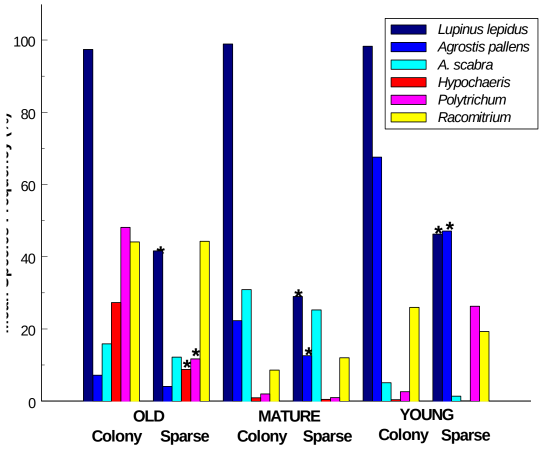


Fig. 1. Mean frequency of representative species in the six transect types. * = frequencies that differ between colonies and sparse sites (P < 0.05, paired t-test). *A. scabra* = *Agrostis scabra*; *Hypochaeris* = *H. radicata*; *Polytrichum* = *P. juniperinum*; *Racomitrium* = *R. canescens*.

Table 1. Mean richness and percent cover in *Lupinus* sites. s. d. = 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).

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
s. d.	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
s. d.	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
s. d.	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
s. d.	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
s. d.	16.3	10.1		5.9	3.4		13.1	9.1	

Frequency, dominance, and diversity. Frequency (%), Simpson dominance (D), and diversity (H') revealed significant patterns (Fig. 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 (Fig. 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 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 (Fig. 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).

H' increased with age when *Lupinus* was included (Fig. 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 young sparse sites. When mosses were also excluded, diversity increased with age both in 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).

Table 2. Summary of nested analyses of variance. The fixed effects are density (2 levels) within age and age (3 levels); while 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.

Basis	Parameter	Source of Variation	F-value	P-value
– *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
– *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
– *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
– *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
– *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

Fig. 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 dense and sparse samples (paired t-tests), while ANOVA indicates strength of overall differences among the six samples of a set.

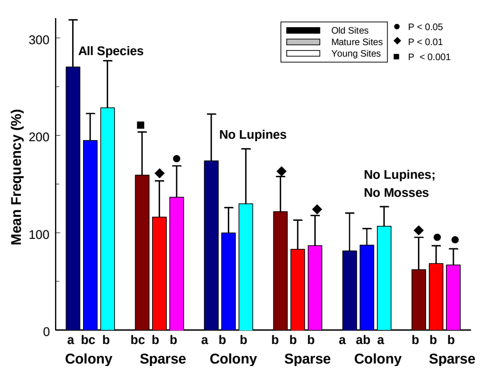


Fig. 3. Dominance index (D), as in Fig. 2.

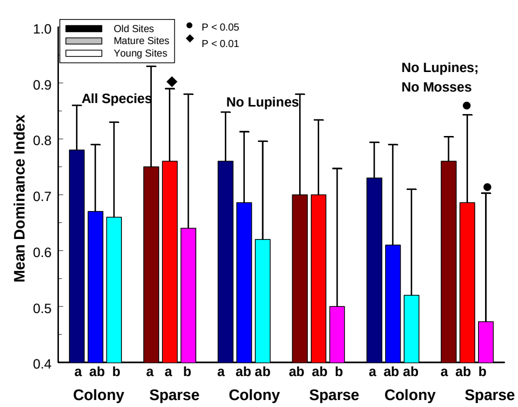
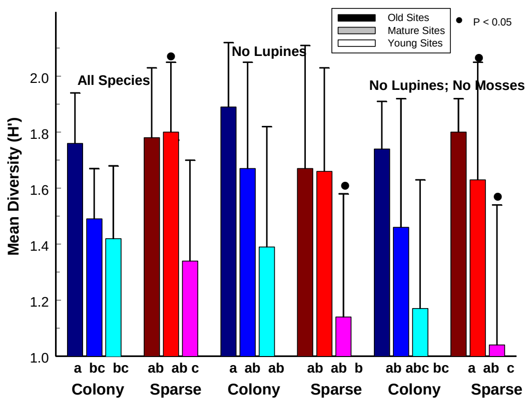


Fig. 4. Diversity (H'), as in Fig. 2.



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.

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

	Quadrats		**Transects**	
Site	**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	$*62.3 \pm 9.89^{cd}$	$*55.5 \pm 10.2^{ab}$	$*47.2 \pm 16.2^{c}$	$*36.3 \pm 19.7^{c}$
Mature Colony	75.4 ± 7.3^{ab}	54.7 ± 9.8^{ab}	69.1 ± 10.6^{ab}	44.5 ± 16.2^{abc}
Mature Sparse	$*52.6 \pm 9.9^{d}$	49.3 ± 11.6^{b}	$*51.8 \pm 12.9^{c}$	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	$*67.8 \pm 6.0^{bc}$	62.0 ± 8.8^{ab}	$*61.2 \pm 13.2^{b}$	54.3 ± 15.8^{a}

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}

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 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, indicated by "∪", 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.

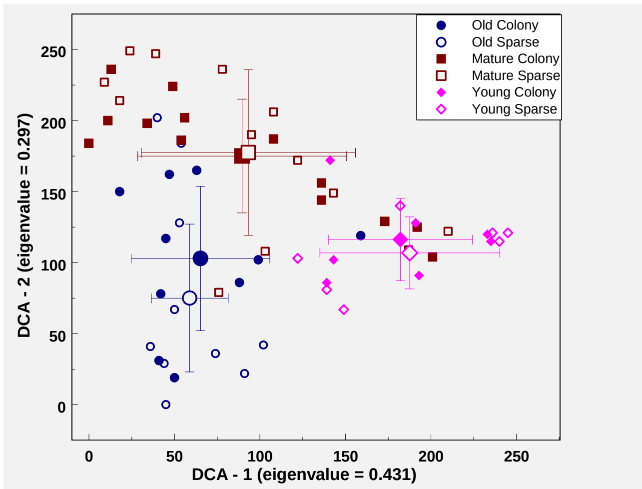
Table 5. Regression of *Lupinus* frequency vs. vegetation structure based on frequency excluding *Lupinus*. All = 1200 quadrats; Sparse = 598 quadrats. "No mosses" indicates regressions based on measures calculated after excluding mosses. (NS=not significant; ∪ = shape of second order relationship with increasing lupine frequency; other values are linear first order regressions).

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	

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 (Fig. 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.

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



Discussion—*Positive and negative effects*

Positive effects associated with *Lupinus* are likely due to improved fertility (Halvorson & 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 & 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.

Most dominant plants alter their immediate environment to affect some species positively and others negatively (Uesada & 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 & 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 & 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 & Morris 1990; Halvorson et al. 2005). Young colonies may promote some species because *Lupinus* cannot suppress established plants, which can, however, 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 & Cárdenas 1995; Poli Marchese & 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 & 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 & 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 & Eckert 2005). Thus, *Lupinus* alone may nudge vegetation development along alternative trajectories both where it is dense and in adjacent sites (c.f. Walker & 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 & Lancaster 1999) within one habitat. Unlike the model of Petraitis & 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.

ESA Field Trip Participants (August 2004)