

## EARLY SUCCESSION ON LAHARS SPAWNED BY MOUNT ST. HELENS<sup>1</sup>

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The effects of isolation on primary succession are poorly documented. I monitored vegetation recovery on two Mount St. Helens lahars (mud flows) with different degrees of isolation using contiguous plots. Seventeen years after the eruption, species richness was stable, but cover continued to increase. That isolation affects community structure was confirmed in several ways. The dominance hierarchies of the lahars differed sharply. Detrended correspondence analysis on Lahar I showed a trend related to distance from an adjacent woodland, whereas vegetation on Lahar II was relatively homogeneous. Spectra of growth forms and dispersal types also differed. Lahar I was dominated by species with modest dispersal ability, while Lahar II was dominated by species with better dispersal. Variation between plots should decline through time, a prediction confirmed on Lahar II. Lahar I remained heterogeneous despite having developed significantly higher cover. Here, the increasing distance from the forest has prevented plots from becoming more homogeneous. At this stage of early primary succession, neither lahar is converging towards the species composition of adjacent vegetation. This study shows that isolation and differential dispersal ability combine to determine initial vegetation structure. Stochastic effects resulting from dispersal limitations may resist the more deterministic effects of competition that could lead to floristic convergence.

**Key words:** dispersal; landscape effects; lahars; Mount St. Helens; primary succession; vegetation structure; volcanoes.

The 1980 eruption of Mount St. Helens created new habitats (del Moral and Bliss, 1993) that included lahars (mud flows). Lahars, caused by rapidly melting ice (Francis, 1993), can devastate huge areas. Halpern and Harmon (1983) described initial invasion on the Muddy River lahar on the east side of Mount St. Helens. They found that richness and cover declined with distance from adjacent forests. Such results suggest that short distances can affect colonization. I have studied two small lahars on the southwest side of Mount St. Helens since 1980. By 1982 there were only five sparsely distributed species (del Moral and Wood, 1988). By 1985 strong cover gradients had developed along transects perpendicular to woodland vegetation (Wood and del Moral, 1988).

This paper describes primary succession on these lahars. Two themes animate this paper. The first concerns recovery patterns and the second concerns the role of isolation on community structure and development. Exploratory analyses suggested three hypotheses: (1) species composition depends on the degree of isolation from sources of colonists; (2) community development gradually reduces compositional heterogeneity; and (3) vegetation structure converges towards that of adjacent vegetation. Tests of each hypothesis are described below.

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## MATERIALS AND METHODS

**Study area**—Two lahars, formed during the 1980 eruption of Mount St. Helens (Cummins, 1981), were monitored. They are on the southwest flank of the volcano. Lahar I is located between 1415 and 1445 m at latitude N 46°10'56", longitude 122°13'7". Lahar II is located between 1430 and 1475 m at latitude N 46°12'06", longitude 122°13'36" (Fig. 1). Both lahars experience summer drought and provide limited nutrients. Lahar I is moderately protected from wind, while Lahar II is more exposed. Limited seed trapping in 1989 revealed that both lahars received < 3 seeds · m<sup>-2</sup> · yr<sup>-1</sup> and had a similar seed rain composition (Wood and del Moral, unpublished data).

The vegetation near these lahars developed on lahars at least 300 yr old. Vegetation includes meadows dominated by *Agrostis diegoensis*, open woodlands dominated by *Abies lasiocarpa* (Hook.) Nutt. and *Pinus contorta* Dougl. var. *latifolia* Engelm. with a variety of herbs, and dense conifer forests with a sparse herb layer. Del Moral and Bliss (1993) described vegetation, soils, and climate in barren zones of Mount St. Helens more fully.

Two comparison sites, located on the Pumice Plain (del Moral, Titus, and Cook, 1995) and the Abraham Plain (del Moral and Wood, 1993), were used. The Pumice Plain is on the north slope of the volcano between 1060 and 1080 m latitude (N 46°15'05", longitude 122°10'42"). It received a seed rain larger than any other site discussed here (D. M. Wood, unpublished data). The Abraham Plain is on the east flank at 1280 m (N 46°12'58", longitude 122°08'15"). It is nearly smooth and received a seed input larger than that of the lahars (D. M. Wood, unpublished data).

Vascular plant nomenclature is based on Hitchcock and Cronquist (1973).

**Sampling**—Grids of permanent plots offer several advantages for succession studies (Austin, 1980). Spatial patterns can be analyzed, sampling problems are minimized, assumptions associated with chronosequences are mitigated, and invasion patterns can be explored (del Moral and Wood, 1993). In 1987, I established a grid of 175 10 × 10 m plots (15 rows of ten plots and five rows of five plots) on Lahar I. The southern edge was uphill, but near a meadow–woodland complex. The distance of the eastern edge to the adjacent woodland increased from 2 to 30 m (Fig. 1). Also in 1987, a grid of 317 10 × 10 m plots

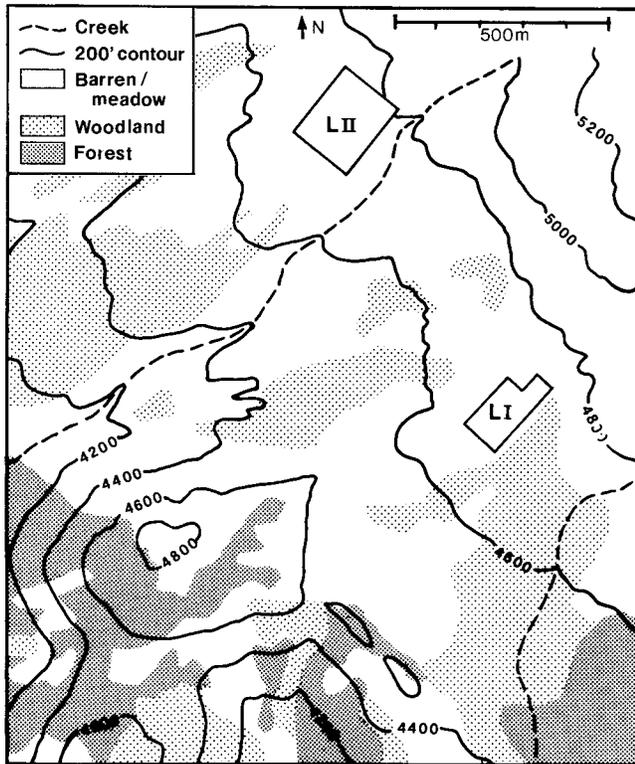


Fig. 1. Location of lahar grids in relationship to intact meadows, open woodland, and forest.

(17 rows of 16 plots and three rows of 15 plots) was established on Lahar II. This lahar is isolated by deep canyons to the east and west. The lahar killed most vegetation within 90 m below the grid, but standing dead trees occur to within 40 m. No vegetation survived within 200 m above the grid. Sources of colonists for Lahar II are over 200 m downhill of the grid (Fig. 1). The Pumice Plain grid consisted of 180 plots and the Abraham Plain grid consisted of 400 plots (del Moral and Wood, 1993).

I used a cover index to estimate dominance. The index is: 1 = one to five plants; 2 = six to 20 plants; 3 = over 20 plants or 0.25 to 0.5% cover; 4 = 0.51 to 1.0% cover; 5 = 1.01 to 2% cover; 6 = 2.01 to 4% cover; and 7 = 4.01 to 8% cover. Cover estimates over 8% were recorded directly. Cover takes precedence over density (e.g., one plant covering 1.5 m<sup>2</sup> would score 5).

Lahar I was sampled annually from 1987 to 1992, and in 1994 and 1996. Lahar II was sampled annually from 1987 to 1991, and in 1993 and 1995. Species richness, total index score, and diversity (*H'*) based on the index scores were calculated for each plot. Total percent cover was estimated by backtransformations. Scores of 1 and 2 were converted based on the size of the species. For example, a score of 1 was

converted to 0.06% for a small species and to 0.12% for a large one. Index scores from 3 to 7 were backtransformed to the midpoint of the index range. For example, index scores of 6 were transformed to 3%.

**Data analyses**—Percentage similarity (PS) robustly determines ecological distance among vegetation samples (Faith, Minchin, and Belbin, 1987). PS was calculated with the MVSP program (Kovach, 1993) and was used to compare data sets within and between years.

$$PS_{ij} = 200 \sum_k \min(X_{ik}, X_{jk}) / \sum_k (X_{ik} + X_{jk}), \quad (1)$$

where *i* and *j* are two samples of *k* species, *X<sub>ik</sub>* and *X<sub>jk</sub>* are the covers of species *k* in each sample, and min = the minimum of these two values.

I calculated the Sørensen matching coefficient (Kovach, 1993):

$$S_{ij} = 2a / (2a + b + c), \quad (2)$$

where *a* is the number of species shared, and *b* and *c* are the number of species in samples *i* and *j*, respectively.

I used detrended correspondence analysis (DCA, Hill and Gauch, 1980), an indirect ordination method, to describe temporal vegetation change on the grids and to estimate differences among composite samples (blocks) from the most recent sampling dates. These blocks consisted of 16 100-m<sup>2</sup> plots in a 4 × 4 array. There were nine blocks on Lahar I arrayed to maximize coverage on the grid (144 of the 175 plots were used). There were 20 blocks on Lahar II arrayed such that all 317 plots were used (block 20 had 13 plots). A DCA of all 29 blocks was conducted without either transformations or down-weighting of rare species.

Changes in the relative abundance of representative species on each lahar were compared. The mean index score is the total score of each species, divided by the number of plots. Frequency is the percentage of plots occupied by the species. Relative cover is the total index score of the species divided by the total index score of the grid. Mean index and frequency describe development of a species, while relative cover describes vegetation dynamics.

Comparisons of all structural indices, species abundance, and DCA scores between years were made using one-way analysis of variance, followed by a comparison of means using the Bonferroni method. This multiple range test is very conservative since the *t* value increases with the number of comparisons (Analytical Software, 1994). I determined linear regressions of DCA axis scores with sample position on the grid using linear regression (Analytical Software, 1994).

RESULTS

**Community structure**—In Tables 1 and 2, I summarize structural changes that occurred on the lahars between 1987 and 1995–96. One-way AOV of each structural trend on both lahars showed significant changes *P* < 0.0001. All reported differences among means were determined using the Bonferroni comparison of means (*P* < 0.05).

Mean richness per 100 m<sup>2</sup> increased significantly on

TABLE 1. Development of community structure on Lahar I, 1987–1996. Means of 175 100-m<sup>2</sup> contiguous plots near an open *Abies lasiocarpa*–*Pinus contorta* woodland. One-way AOV indicated that all structural measures tested changed significantly (*P* < 0.05). Row values with the same superscript letter are not significantly different using the Bonferroni comparison of means (*P* < 0.05).

Characteristic	Year						
	1987	1988	1989	1991	1992	1994	1996
Total richness	31	35	35	41	48	49	51
Mean richness	8.4 <sup>a</sup>	9.8 <sup>b</sup>	11.3 <sup>c</sup>	12.9 <sup>d</sup>	15.0 <sup>e</sup>	15.9 <sup>f</sup>	16.4 <sup>f</sup>
Mean cover index	13.6 <sup>a</sup>	17.1 <sup>b</sup>	20.8 <sup>c</sup>	25.2 <sup>d</sup>	31.8 <sup>e</sup>	38.9 <sup>f</sup>	52.3 <sup>g</sup>
Mean cover percent	1.57 <sup>a</sup>	2.39 <sup>ab</sup>	3.22 <sup>ab</sup>	4.08 <sup>b</sup>	8.74 <sup>c</sup>	10.03 <sup>d</sup>	24.04 <sup>e</sup>
Diversity ( <i>H'</i> )	1.79 <sup>a</sup>	1.79 <sup>a</sup>	1.84 <sup>a</sup>	1.91 <sup>a</sup>	1.75 <sup>a</sup>	1.80 <sup>a</sup>	1.38 <sup>b</sup>

TABLE 2. Development of community structure on Lahar II, 1987–1995. Mean values are from 317 100-m<sup>2</sup> contiguous plots. One-way AOV indicated that all structural measures tested changed significantly ( $P < 0.05$ ). Row values with the same superscript letter are not significantly different using the Bonferroni comparison of means ( $P < 0.05$ ).

Characteristic	Year						
	1987	1988	1989	1990	1991	1993	1995
Total richness	31	33	35	37	43	48	50
Mean richness	7.2 <sup>a</sup>	10.0 <sup>b</sup>	11.9 <sup>c</sup>	12.6 <sup>d</sup>	14.2 <sup>e</sup>	15.7 <sup>f</sup>	16.0 <sup>f</sup>
Mean cover index	9.4 <sup>a</sup>	15.2 <sup>b</sup>	17.3 <sup>c</sup>	21.9 <sup>d</sup>	24.3 <sup>e</sup>	29.7 <sup>f</sup>	37.1 <sup>g</sup>
Mean cover percent	0.9 <sup>a</sup>	1.86 <sup>b</sup>	1.97 <sup>b</sup>	2.69 <sup>c</sup>	2.76 <sup>c</sup>	3.16 <sup>c</sup>	5.16 <sup>d</sup>
Diversity ( $H'$ )	1.86 <sup>a</sup>	1.98 <sup>b</sup>	2.21 <sup>cd</sup>	2.10 <sup>bc</sup>	2.22 <sup>de</sup>	2.40 <sup>e</sup>	2.08 <sup>bc</sup>

both lahars during the study. At the last survey, there were ~ 50 species on each lahar, of which half were common. Species richness leveled off since 1992–1993. The recent small increments were due to rare species.

The mean cover index scores and mean percentage cover both increased significantly on both lahars. Recent cover increases were due to rapid increases in conifer cover and the spread of species such as *Polygonum newberryi* Small, *Luetkea pectinata* (Pursh.) Kuntze, *Penstemon cardwellii* Howell, and *Agrostis diegoensis* Vasey, which have strong lateral growth. Lahar I had higher cover (~24%); however it also remained open with substantial room for expansion and immigration. Conifer saplings were dominant. Lahar II was still sparsely vegetated (cover ~ 5%) 15 yr after the eruption.

Diversity ( $H'$ ) changed little on Lahar I until the significant decline in 1996 due to increased *Abies* and *Pinus* dominance.  $H'$  on Lahar II was significantly higher than on Lahar I due to greater equitability among the species.

**Species patterns**—Tables 3 (Lahar I) and 4 (Lahar II) summarize changes in mean cover index, frequency, and relative cover of common species since 1987. Significant cover index differences between sample years were determined by one-way AOV followed by a Bonferroni comparison of means.

*Abies lasiocarpa* and *Pinus contorta* (not shown) dominance began to increase rapidly on Lahar I after 1993. Increases on Lahar II were less pronounced. Cover of *Agrostis diegoensis*, *Luetkea pectinata*, and *Polygonum newberryi* on both lahars and *Penstemon cardwellii* on Lahar II continued to increase during this study. *Polygonum* and *Penstemon* were the dominant ground-layer species on Lahar II. *Anaphalis margaritacea* (L.) B. & H., *Hieracium albiflorum* Hook., *H. gracile* Hook. (not shown), and *Hypochaeris radicata* L. (not shown) were widespread pioneers on both lahars, but none reached the dominance they achieved on more isolated sites on the volcano (del Moral and Bliss, 1993). *Aster ledophyllus* Gray occurred on both lahars, but it was not common on Lahar I (not shown), which is traversed by elk. Elks browse *Aster* heavily (Wood and del Moral, 1987), which may lead to the observed *Aster* cover differences. *Juncus parryi* Engelm. produces tiny seeds and readily invades isolated sites. Along with *Carex rossii* Boott, it continued to expand from sites of initial establishment on both lahars. *Eriogonum pyrolifolium* Hook. and *Spraguea umbellata* Torr. are stress-tolerant species that expanded quickly from a few initially colonized sites. *Lupinus lepidus* Dougl. was the first species observed on both lahars.

Its cover fluctuated greatly because individuals of this species are short lived.

**Hypothesis 1**—Species composition depends on the degree of isolation. If true, these lahars should be structurally distinct from each other, from isolated sites, and from adjacent mature vegetation. These predictions follow.

Similarity between sites is inversely related to their degree of isolation. Mean index scores on Lahar I, Lahar II, on the Pumice Plain (1996) and on Abraham Plain (1996) were compared using PS of relative cover (Table 5, lower half) and the Sørensen's coefficient (Table 5, upper half). The two Plains grids were similar to each other, but distinct from the lahars. Each was more similar to Lahar II than to Lahar I. Sørensen's index ( $S$ ) also indicated that the Plains were distinct from the lahars, while the lahars were floristically similar to each other ( $S = 0.977$ ), despite having a PS = 63.5%. These results demonstrate that the effects of isolation can be observed on a scale of a few hundred m.

Differential isolation causes lahars to be distinct. Fig. 2 shows the DCA distribution of composite samples (blocks) of both lahars. Variation was concentrated on the first axis (54.1%), rendering analyses of other axes fruitless. On DCA-1, Lahar I scores ranged from 0.0 to 0.75 (mean =  $0.41 \pm 0.27$ ). On Lahar II they ranged from 1.16 to 1.51 (mean =  $1.35 \pm 0.10$ ). The means were significantly different ( $t$  test,  $P < 0.0001$ ). Low DCA-1 values were associated with high values of conifers, species common in the nearby woodland (e.g., *Lomatium martindalei* Coult. & Rose and *Fragaria virginiana* Duchesne). High DCA-1 values were associated with species adapted to drier, more open sites (e.g., *Arctostaphylos nevadensis* Gray, *Eriogonum pyrolifolium*, and *Hieracium albiflorum*.)

There was a direct relationship between the DCA-1 score and block distance from the woodland. On Lahar I, the two blocks nearest the forest had scores of 0.0 and 0.03; the two blocks over 100 m from the forest had scores of 0.68 and 0.75. On Lahar II, this pattern was weak. The least isolated blocks had DCA-1 scores between 1.16 and 1.32, while the most isolated blocks had scores greater than 1.50.

This spatial relationship was confirmed by analysis of these 1996 Lahar I plots: all 20 plots in first and fifth grid columns and all 15 plots in the tenth grid column. DCA-1 values were least in column 1 (0.45), intermediate in column 5 (0.63), and highest in column 10 (1.08). Columns 1 and 5 were not statistically different, but col-

TABLE 3. Changes in mean cover index, frequency, and relative cover for 12 common species on Lahar I. (Sample size = 175 contiguous 100-m<sup>2</sup> plots.) One-way AOV indicated that all species changed significantly ( $P < 0.05$ ). Index values with the same superscript letter are not significantly different using the Bonferroni comparison of means ( $P < 0.05$ ).

Species, Attributes	Year				
	1987	1989	1992	1994	1996
<i>Abies lasiocarpa</i>					
Mean index score	3.12 <sup>a</sup>	4.00 <sup>b</sup>	6.63 <sup>c</sup>	6.74 <sup>c</sup>	13.81 <sup>d</sup>
Frequency	99	99	100	100	100
Relative cover	22.71	19.20	19.25	17.34	23.34
<i>Agrostis diegoensis</i>					
Mean index score	0.44 <sup>a</sup>	0.72 <sup>a</sup>	1.28 <sup>b</sup>	1.73 <sup>c</sup>	2.06 <sup>d</sup>
Frequency	42	62	80	82	82
Relative cover	3.23	3.46	4.05	4.45	3.94
<i>Anaphalis margaritacea</i>					
Mean index score	0.5 <sup>a</sup>	0.85 <sup>b</sup>	1.17 <sup>c</sup>	1.03 <sup>cd</sup>	1.64 <sup>d</sup>
Frequency	46	66	79	76	86
Relative cover	3.69	4.09	3.68	2.26	3.14
<i>Carex rossii</i>					
Mean index score	0.45 <sup>a</sup>	0.60 <sup>b</sup>	0.90 <sup>c</sup>	0.92 <sup>c</sup>	0.86 <sup>c</sup>
Frequency	43	60	80	82	82
Relative cover	3.27	2.88	2.82	2.36	1.65
<i>Eriogonum pyrolifolium</i>					
Mean index score	0.49 <sup>a</sup>	0.67 <sup>a</sup>	1.05 <sup>b</sup>	1.38 <sup>c</sup>	1.43 <sup>c</sup>
Frequency	47	57	76	81	82
Relative cover	3.60	3.21	3.29	2.54	2.74
<i>Hieracium albiflorum</i>					
Mean index score	0.25 <sup>a</sup>	0.36 <sup>a</sup>	0.71 <sup>b</sup>	0.99 <sup>b</sup>	1.11 <sup>c</sup>
Frequency	24	36	67	83	80
Relative cover	1.80	1.73	2.24	2.54	2.13
<i>Juncus parryi</i>					
Mean index score	0.78 <sup>a</sup>	1.19 <sup>b</sup>	1.81 <sup>c</sup>	2.56 <sup>d</sup>	2.47 <sup>d</sup>
Frequency	70	83	95	97	96
Relative cover	5.70	5.73	5.69	6.58	4.72
<i>Luetkea pectinata</i>					
Mean index score	1.48 <sup>a</sup>	2.21 <sup>b</sup>	3.54 <sup>c</sup>	3.83 <sup>cd</sup>	4.10 <sup>d</sup>
Frequency	92	97	98	99	99
Relative cover	10.85	10.59	11.13	9.86	7.83
<i>Lupinus lepidus</i>					
Mean index score	1.73 <sup>a</sup>	1.95 <sup>a</sup>	2.59 <sup>b</sup>	1.67 <sup>a</sup>	2.35 <sup>b</sup>
Frequency	89	94	97	97	98
Relative cover	12.65	9.38	8.13	4.30	4.49
<i>Penstemon cardwellii</i>					
Mean index score	0.26 <sup>a</sup>	0.33 <sup>a</sup>	0.85 <sup>b</sup>	1.24 <sup>c</sup>	1.31 <sup>c</sup>
Frequency	22	28	51	58	62
Relative cover	1.93	1.56	2.68	3.19	2.51
<i>Polygonum newberryi</i>					
Mean index score	1.03 <sup>a</sup>	1.93 <sup>b</sup>	2.39 <sup>b</sup>	3.06 <sup>c</sup>	3.64 <sup>d</sup>
Frequency	60	83	91	94	97
Relative cover	7.54	9.27	7.50	7.87	6.96
<i>Spraguea umbellata</i>					
Mean index score	0.14 <sup>a</sup>	0.44 <sup>b</sup>	1.13 <sup>c</sup>	1.94 <sup>d</sup>	1.79 <sup>d</sup>
Frequency	14	36	72	80	82
Relative cover	1.01	2.11	3.55	4.99	3.42

umn 10 was different from both ( $t$  test,  $P < 0.02$ ). The multiple regression of DCA-1 vs.  $X$  and  $Y$  was highly significant ( $R^2 = 0.72$ ;  $F = 67.49$ ;  $P < 0.0001$ ). The regression equation is  $DCA-1 = -0.016 + 0.049x + 0.067y$ .

TABLE 4. Changes in mean cover index, frequency, and relative cover for 13 common species on Lahar II. (Sample size = 317 contiguous 100-m<sup>2</sup> plots.) One-way AOV indicated that all species changed significantly ( $P < 0.05$ ). Index values with the same superscript letter are not significantly different using the Bonferroni comparison of means ( $P < 0.05$ ).

Species, Attributes	Year				
	1987	1989	1991	1993	1995
<i>Abies lasiocarpa</i>					
Mean index score	1.19 <sup>a</sup>	1.47 <sup>b</sup>	1.83 <sup>c</sup>	2.56 <sup>d</sup>	2.88 <sup>e</sup>
Frequency	88	95	98	99	98
Relative cover	12.70	8.49	7.51	8.62	7.76
<i>Agrostis diegoensis</i>					
Mean index score	0.36 <sup>a</sup>	0.69 <sup>b</sup>	1.09 <sup>c</sup>	1.68 <sup>d</sup>	1.97 <sup>e</sup>
Frequency	33	59	77	92	93
Relative cover	3.86	3.97	4.49	5.66	5.31
<i>Anaphalis margaritacea</i>					
Mean index score	0.50 <sup>a</sup>	0.94 <sup>b</sup>	1.14 <sup>c</sup>	1.36 <sup>d</sup>	1.77 <sup>e</sup>
Frequency	34	67	81	89	93
Relative cover	5.34	5.43	4.68	4.59	4.76
<i>Aster ledophyllus</i>					
Mean index score	0.66 <sup>a</sup>	0.99 <sup>b</sup>	1.33 <sup>c</sup>	1.28 <sup>c</sup>	1.29 <sup>c</sup>
Frequency	41	70	78	85	85
Relative cover	7.02	5.7	5.47	4.32	3.46
<i>Carex rossii</i>					
Mean index score	0.44 <sup>a</sup>	0.67 <sup>b</sup>	0.70 <sup>bc</sup>	0.85 <sup>c</sup>	0.86 <sup>c</sup>
Frequency	37	54	61	60	61
Relative cover	4.64	3.88	2.89	2.85	2.31
<i>Eriogonum pyrolifolium</i>					
Mean index score	0.76 <sup>a</sup>	1.01 <sup>b</sup>	1.67 <sup>c</sup>	2.39 <sup>d</sup>	3.41 <sup>e</sup>
Frequency	67	81	91	97	97
Relative cover	8.13	5.83	6.87	8.25	9.17
<i>Hieracium albiflorum</i>					
Mean index score	0.26 <sup>a</sup>	0.60 <sup>b</sup>	0.88 <sup>b</sup>	1.21 <sup>c</sup>	1.34 <sup>d</sup>
Frequency	26	57	81	97	97
Relative cover	2.76	3.44	3.60	4.06	3.60
<i>Juncus parryi</i>					
Mean index score	0.55 <sup>a</sup>	0.99 <sup>b</sup>	1.07 <sup>b</sup>	1.84 <sup>c</sup>	2.08 <sup>d</sup>
Frequency	49	69	78	95	95
Relative cover	5.81	5.74	4.41	6.19	5.60
<i>Luetkea pectinata</i>					
Mean index score	0.44 <sup>a</sup>	1.04 <sup>b</sup>	1.51 <sup>c</sup>	1.74 <sup>c</sup>	2.61 <sup>d</sup>
Frequency	40	78	86	91	93
Relative cover	4.64	5.99	6.21	5.88	7.03
<i>Lupinus lepidus</i>					
Mean index score	1.11 <sup>a</sup>	2.15 <sup>b</sup>	2.83 <sup>d</sup>	1.97 <sup>c</sup>	2.15 <sup>b</sup>
Frequency	76	96	99	99	99
Relative cover	11.83	12.44	11.64	6.63	5.77
<i>Penstemon cardwellii</i>					
Mean index score	0.79 <sup>a</sup>	1.32 <sup>b</sup>	2.42 <sup>c</sup>	3.04 <sup>d</sup>	4.33 <sup>e</sup>
Frequency	68	79	89	100	100
Relative cover	8.47	7.64	9.96	10.25	11.66
<i>Polygonum newberryi</i>					
Mean index score	1.23 <sup>a</sup>	2.46 <sup>b</sup>	2.98 <sup>c</sup>	3.30 <sup>d</sup>	5.11 <sup>e</sup>
Frequency	59	97	95	99	99
Relative cover	13.07	14.19	12.27	11.11	13.76
<i>Spraguea umbellata</i>					
Mean index score	0.17 <sup>a</sup>	0.65 <sup>b</sup>	1.26 <sup>c</sup>	1.81 <sup>d</sup>	1.95 <sup>e</sup>
Frequency	16	55	82	95	96
Relative cover	1.81	3.75	5.20	6.09	5.24

TABLE 5. Percentage similarity (lower half) and Sørensen's Index (top half) among Lahar, Abraham Plain, and Pumice Plain grids that differ in their degrees of isolation. Similarity is based on relative composition. Sites are arrayed in order of decreasing isolation.

Site	AP-96	PP-96	Lahar II	Lahar I
PA-96	—	0.941	0.835	0.810
PP-96	61.3%	—	0.831	0.805
Lahar II	38.1%	43.9%	—	0.977
Lahar I	26.6%	32.7%	60.7%	—

These results are consistent with the prediction that differential isolation affects species composition differences between lahars. Differences on Lahar I suggest that composition may be affected by distances of <50 m.

Isolation affects growth form spectra. Lahar I should have more species with strong vegetative growth because such species typically have inefficient seed dispersal (Tsuyuzaki and del Moral, 1995; Tilman, Lehman, and Yin, 1997). Lahar II should be dominated by composites and graminoids with better dispersal abilities. Species from the two lahars were aggregated into nine growth forms, omitting species with less than five occurrences. The mean cover indices of growth forms on the two lahars from 1987 to 1996 are shown in Table 6. The abundance of each growth form increased sequentially. However, growth form proportions differed between lahars. Conifers dominated Lahar I, but not Lahar II, where the Asteraceae/Onagraceae category was more abundant. The other forb category was dominated by species with strong lateral spread, such as *Polygonum*, and by stress-tolerant species such as *Eriogonum*. This category was most abundant on Lahar II. The absolute covers of other categories were similar. These patterns agreed with the prediction that growth form spectra would be affected by isolation.

Isolation affects the dispersal ability spectrum. While growth forms are unambiguous, they are not directly related to dispersal ability. I categorized the species used above into five dispersal ability categories (poor, modest, moderate, good, and excellent) based on frequency in seed traps (D. M. Wood, unpublished data) and seed sizes (Wood and del Moral, 1987; Tsuyuzaki and del Moral, 1995). These results are summarized in Fig. 3. On both lahars, the small poor dispersal group increased slightly

through time, due to the vegetative expansion of *Agrostis diegoensis*. Good dispersers were initially abundant, but their relative abundance declined on Lahar I. Proportions of other groups did not change dramatically.

There were marked differences between the lahars. Modest dispersers were twice as abundant on Lahar I as on Lahar II, while moderate, good, and excellent dispersers all were more abundant on Lahar II. The most common species on Lahar I were modest dispersers, the most common on Lahar II were good dispersers.

Dispersal type spectra differ more strikingly between the four grids (Table 7). Abraham Plain was dominated by excellent dispersers, while good and excellent dispersers dominated the Pumice Plain.

Results at both scales support the prediction that isolation forms a selective dispersal barrier thus affecting the dispersal type spectrum.

**Hypothesis 2**—Community development reduces compositional heterogeneity. Through time, more plants establish from distant sources, established plants spread, and locally produced seeds disperse to adjacent plots. The tests involve successive measurements of between-sample variation.

DCA axis scores become less variable through time. The 29 blocks described above were analyzed for changes in variation through time. The nine Lahar I blocks were analyzed in 1987, 1988, 1991, 1994, and 1996; the 20 Lahar II blocks were analyzed in 1987, 1988, 1991, 1993, and 1995. The mean ( $\pm$  SD) DCA-1 and DCA-2 scores were calculated. In Table 8, Bonferroni comparison of means was used to assess differences between means ( $P < 0.05$ ).

Both the mean DCA-1 and DCA-2 scores for Lahar I showed a small significant increase through time. However, homogeneity, determined by reduced standard deviations, did not increase on either axis. Lahar II showed significant increasing DCA-1 scores and declining variability on both axes. On both lahars, the shifts in mean DCA positions correlated with increases in more mesophytic species such as *Carex phaeocephala* Piper, *C. limnophila* Herman, *Danthonia intermedia* Vasey, *Juncus mertensianus* Bong., *Lupinus latifolius* Agaradh., ferns, and mosses.

On Lahar II plots are becoming homogeneous, such

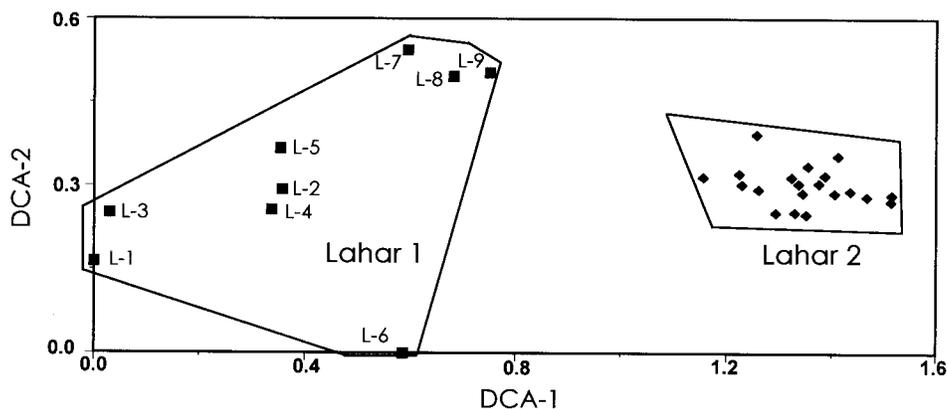


Fig. 2. DCA of nine composite 1996 Lahar I plots (L-n) and 20 composite 1995 Lahar II plots (Lahar II).

TABLE 6. Mean cover index, by growth form, based on species with at least four occurrences. Percentages are based on the totals for the species used (*N* is the number of species in each growth form).

Growth form	<i>N</i>	Site	Cover					Percentages
			1987	1989	1991–1992	1993–1994	1995–1996	1995–1996
Trees	2	Lahar I	5.02	6.66	8.87	11.11	20.61	42.3
	2	Lahar II	1.48	1.88	2.50	3.50	4.36	11.8
Evergreen shrubs	3	Lahar I	1.79	2.61	4.86	5.57	5.97	12.3
	3	Lahar II	1.23	2.36	3.94	4.79	6.95	18.8
Deciduous shrubs	2	Lahar I	0.03	0.05	0.13	0.18	0.31	0.6
	1	Lahar II	0.01	0.04	0.09	0.13	0.15	0.4
Asteraceae/ Onagraceae	8	Lahar I	1.14	2.35	3.71	4.08	4.69	9.6
	8	Lahar II	1.73	3.73	4.94	5.54	6.21	16.8
Other forbs	7	Lahar I	3.63	5.64	8.11	9.10	10.47	21.5
	7	Lahar II	3.42	6.58	9.17	10.08	13.16	35.6
Poaceae	3	Lahar I	0.46	0.75	1.47	1.98	2.37	4.9
	4	Lahar II	0.41	0.91	1.55	2.53	3.03	8.2
Other graminoids	5	Lahar I	1.37	1.93	2.94	3.86	3.73	7.7
	5	Lahar II	0.20	1.72	1.93	2.77	3.05	8.2
Ferns	2	Lahar I	0	0.01	0.17	0.18	0.23	0.5
	2	Lahar II	0.00	0.00	0.003	0.006	0.015	<0.1
Mosses	1	Lahar I	0	0	0.23	0.25	0.29	0.6
	1	Lahar II	0.00	0.00	0.02	0.03	0.08	0.2

that DCA scores became less variable. In contrast, on Lahar I systematic changes in species composition associated with distance from the woodland appeared to override tendencies towards homogenization. Samples from opposite ends of the grid typically remain as distinct as they had been initially.

Small-scale heterogeneity declines through time. Changing heterogeneity on the lahars was determined at

a smaller scale using PS from two sets of 20 100-m<sup>2</sup> plots on each grid. The first set was determined randomly, provided that no selected plot was within two plots of another. Each plot of the second set was next to one of the first set, selected randomly from the four possibilities so as to avoid contact with any other plot. The mean PS of each plot compared to all others on each lahar in each year was calculated and PS differences between years determined by the Bonferroni comparison of means (*P* < 0.05). Increased similarity implies reduced heterogeneity (Table 9).

The results of “random” and “next” plots were similar. On Lahar I, similarity increased initially, but changed inconsistently thereafter. On Lahar II, similarity increased steadily. Early Lahar II samples were more heterogeneous than those of Lahar I (45 vs. 58%), while the latest samples were more homogeneous (72 vs. 65%). There remains substantial variation on Lahar I that may be due to dispersal effects. All samples on Lahar II were sufficiently isolated that they were essentially equidistant from sources and are becoming more homogeneous.

Resemblance among lahar samples decreases with time between sample dates. If samples become more similar, the most recent sample should be less similar to the first sample than to the next most recent sample. Lahar I showed this trend except in 1996 (Table 10). The results

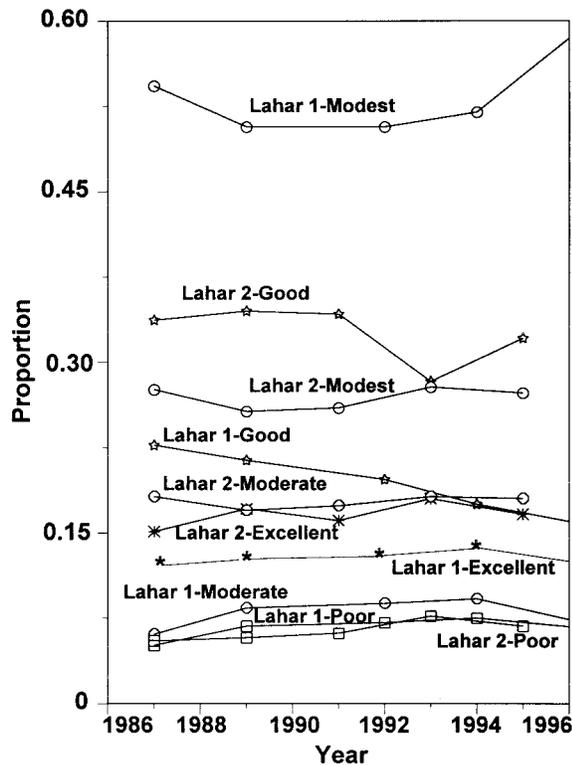


Fig. 3. Proportions of each of five dispersal categories on both lahars. The categories are poor, modest, moderate, good, and excellent dispersers.

TABLE 7. Percentage of each dispersal ability category on grids, based on the most recent sampling period. (Pumice Plain and Abraham Plain based on unpublished data.) Boldfaced values highlight modal categories.

Dispersal category	Lahar I	Lahar II	Pumice	Abraham
Poor	6.8	6.8	5.1	8.8
Modest	<b>58.5</b>	<b>27.2</b>	19.5	20.7
Moderate	7.4	18.0	14.8	6.7
Good	16.0	<b>32.1</b>	<b>23.9</b>	13.8
Excellent	11.5	16.6	<b>36.7</b>	<b>50.0</b>

TABLE 8. Mean ( $\pm$  SD) DCA positions for nine blocks (composite samples) from Lahar I and for 20 blocks from Lahar II in the years indicated. All species were employed in these analyses. Values in the same column with the same superscript letter are not significantly different using the Bonferroni comparison of means ( $P < 0.05$ ). "Variance" is the explained variance associated with each axis. (Values are times 1000.)

Year	Lahar I		Year	Lahar II	
	DCA-1	DCA-2		DCA-1	DCA-2
1987	169 $\pm$ 175 <sup>a</sup>	191 $\pm$ 112 <sup>a</sup>	1987	244 $\pm$ 138 <sup>a</sup>	260 $\pm$ 186 <sup>a</sup>
1988	180 $\pm$ 128 <sup>a</sup>	202 $\pm$ 130 <sup>ab</sup>	1988	193 $\pm$ 118 <sup>a</sup>	336 $\pm$ 159 <sup>a</sup>
1991	378 $\pm$ 132 <sup>ab</sup>	297 $\pm$ 204 <sup>ab</sup>	1991	363 $\pm$ 128 <sup>b</sup>	327 $\pm$ 168 <sup>a</sup>
1994	602 $\pm$ 235 <sup>b</sup>	363 $\pm$ 124 <sup>b</sup>	1993	576 $\pm$ 106 <sup>c</sup>	288 $\pm$ 175 <sup>a</sup>
1996	503 $\pm$ 187 <sup>b</sup>	360 $\pm$ 121 <sup>ab</sup>	1995	606 $\pm$ 52 <sup>c</sup>	252 $\pm$ 104 <sup>a</sup>
Variance	30.2	8.6		17.8	9.7

from Lahar II agreed with the prediction. The highest similarity occurred between the two most recent samples.

Most tests supported predictions based on the hypothesis that compositional heterogeneity declines through time. The exception occurred where steep dispersal gradients sustained differences among plots of the Lahar I grid.

**Hypothesis 3**—Vegetation structure converges towards that of adjacent vegetation. Peet (1992) suggested that if this was true, then intersite compositional differences should decline through time. A fair test on these lahars must wait for conifer dominance to shade the site and alter soils. The lahars were compared to adjacent vegetation to illuminate an aspect of succession and provide a baseline for future studies.

Two meadows south and west of Lahar I (sampled in 1994), open woodland vegetation south of Lahar I (1994), and two denser woodlands east of Lahar I (1995) were each sampled with 20 100-m<sup>2</sup> plots. Table 11 summarizes the PS between each lahar over time and the five mature vegetation samples.

All mature vegetation was impacted by up to 15 cm of coarse tephra in 1980, but by no other significant volcanic impacts since  $\sim$  1700 when large lahars covered these areas (del Moral, 1983). Nearby permanent plot vegetation has been stable since 1984 (del Moral, 1993).

Similarity of Lahar I to the woodlands was moderate, but its similarity to the meadow vegetation was low. Similarity to the closed woodland may be increasing due to increasing conifer dominance. Similarity to the open woodland was stable.

Lahar II was more similar to the meadows than to woodlands, but was not converging. The increasing importance of conifers, shrubs, and certain forbs argues

TABLE 9. Mean percentage similarity among 20 randomly selected 100-m<sup>2</sup> plots on each lahar and among 20 plots next to those random plots. (The same plots were used in each year.) Values in the same column with the same superscript letter are not significantly different using the Bonferroni comparison of means ( $P < 0.05$ ).

Year	Lahar I		Year	Lahar II	
	Random	Next		Random	Next
1987	56.8 <sup>a</sup>	60.4 <sup>a</sup>	1987	45.1 <sup>a</sup>	44.5 <sup>a</sup>
1989	64.5 <sup>c</sup>	63.8 <sup>b</sup>	1989	60.8 <sup>b</sup>	54.2 <sup>b</sup>
1992	64.5 <sup>c</sup>	68.3 <sup>c</sup>	1991	63.2 <sup>b</sup>	57.3 <sup>b</sup>
1994	61.9 <sup>b</sup>	65.3 <sup>b</sup>	1993	68.8 <sup>c</sup>	67.6 <sup>c</sup>
1996	65.7 <sup>c</sup>	64.8 <sup>b</sup>	1995	73.4 <sup>d</sup>	70.2 <sup>c</sup>

against convergence to meadows. Similarity to the closed woodland was low and stable. Data from Lahar II do not support Hypothesis 3.

## DISCUSSION

These analyses support the general hypothesis that spatial relationships affect early species composition in plant communities. Spatial effects were manifested within 50 m (cf. Primack and Miao, 1992) and may constitute a source of unexplained variation in mature communities (cf. McCune and Allen, 1985). Dispersal gradients increase spatial variation within a "treatment" (in this case one lahar; see Hurlbert, 1984; Hefner, Butler, and Reilly, 1996). In this study, spatial effects were found at the scale of plots (10 m), blocks (40 m), and grids (over 200 m).

The pace of colonization, estimated from species accumulation, is slackening (cf. Christensen and Peet, 1984; van der Maarel, 1988; Peet, 1992; Myster and Pickett, 1994). Mean species richness is nearly stable, despite continued secondary dispersal from established plants. Strong vegetative growth and secondary dispersal have combined to produce continued cover increases. The vegetation structure of Lahar I will change dramatically as conifers alter environmental conditions and attract birds, thus facilitating dispersal. Species adapted to open conditions will decline, while shade-tolerant species such as *Pedicularis racemosa* Dougl. will begin colonization. Species such as *Lupinus latifolius*, *Phyllodoce empetri-formis* Sw. D. Don., and *Vaccinium membranaceum* Dougl. will become more abundant. Current dominants will persist in gaps until the conifer canopy is nearly closed. This may require several decades on Lahar I and over a century on Lahar II.

**Spatial effects on species composition**—The DCA of blocks with 1995/1996 data showed Lahar I to be structurally distinct from Lahar II. Within-lahar variation was

TABLE 10. Percentage similarity among composite grids, based on relative species composition to emphasize changes in relative positions.

Lahar I	Lahar I				Lahar II	Lahar II			
	1987	1988	1991	1994		1987	1988	1991	1993
1988	92.5	—	—	—	1988	88.6	—	—	—
1991	87.8	87.0	—	—	1991	86.6	91.4	—	—
1994	80.8	81.9	86.9	—	1993	83.7	81.5	85.3	—
1996	85.0	90.1	82.8	85.4	1995	80.7	79.4	84.2	92.4

TABLE 11. Percentage similarity between intact vegetation and Lahar I and Lahar II, based on relative scores in each set of data. Adjacent vegetation is nearby mature vegetation sampled in 2 100-m<sup>2</sup> plots.

Adjacent vegetation	Lahar I					Lahar II				
	1987	1988	1991	1994	1996	1987	1988	1991	1993	1995
Meadow 1	39.7	38.7	43.7	38.2	34.5	48.7	48.0	50.1	47.0	44.0
Meadow 2	42.6	43.7	46.9	41.8	37.4	54.9	52.3	53.4	51.7	48.7
Woods 1	53.5	58.6	47.7	48.1	60.9	32.4	28.9	26.5	28.5	28.2
Woods 2	53.9	58.7	48.1	50.1	60.6	33.7	30.5	28.1	31.7	30.8
Woods 3	57.6	60.2	55.7	61.5	59.9	51.9	51.3	48.1	51.2	49.1

Note: Woods 1 and 2 are closed woods, while Woods 3 is more open.

much greater on Lahar I than on Lahar II. This spatial variation suggested that distances < 50 m are sufficient to alter community structure. On Lahar II, spatial trends were not evident, suggesting that isolation by canyons, elevation, and a distance of over 200 m from seed sources resulted in each plot having nearly equal (and low) probabilities of receiving colonists.

The four grids form an isolation gradient. The proportions of the five dispersal types imply that isolation affects species types. The lahars are at higher elevations and are less isolated than either the Pumice Plain or the Abraham Plain. Pumice Plain is at the lowest elevation, receives more long-distance dispersers, and is near small refugia (del Moral, Titus, and Cook, 1995). Abraham Plain is the most stressful and isolated of the grids (del Moral and Wood, 1993). Some of the floristic and structural differences must relate to differences in stress, but the floristic, growth form (Table 6), and dispersal type patterns observed suggest that isolation also is important. The lahars differed from each other in ways that agree with predictions based on differential isolation. Lahar I was dominated by modest dispersers, while Lahar II was dominated by moderate to excellent dispersers.

**Heterogeneity**—Vegetation in the early stages of primary succession develops by species accrual and by biomass accumulation. Initially, local habitat variation and chance produce variable samples. As some species achieve dominance, sample variation should decline (cf. Myster and Pickett, 1994). No decline should occur if environmental gradients or distance effects predominate.

Temporal changes in vegetation heterogeneity were estimated on these lahars from mean DCA scores in blocks and mean percentage similarity among plots. Among-block variation on Lahar I did not decline, while on Lahar II it did. The standard deviation of Lahar II DCA-I scores was always less than that of Lahar I. There were no apparent environmental differences at the scale of these plots. The Lahar I result implies that distance within the grid alone maintains between-plot heterogeneity since distances are large relative to distances from colonist sources.

Mean PS values substantiate this pattern. Despite increasing conifer dominance, percentage similarity on Lahar I did not increase, while on Lahar II it did. Further, in the last sample year, PS among Lahar II plots was larger than that of Lahar I plots. There do not appear to be large spatial or environmental gradients operating within Lahar II.

**Convergence**—Both convergence and divergence have been observed during succession (Glenn-Lewin and van der Maarel, 1992; Inouye and Tilman, 1995). Evidence from the lahars related to this hypothesis is equivocal due to the early stage of succession. The lack of convergence does not preclude future convergence. Lahar I may be starting to become more similar to the adjacent woodland as conifers become dominant, and appears to be diverging from the surrounding meadow vegetation. Lahar II was more similar to the meadows than to the woods, but no convergence was observed. The vegetation is developing under novel biogeographic conditions that include lahar size, proximity to potential colonists, and the presence of exotic species. This vegetation may remain distinct from both meadow and woodlands indefinitely because most of the colonists are persistent (cf. Gray, 1993). Lahar II vegetation continues to develop, but at a slowing rate. Because its structure differs significantly from that on Lahar I, this vegetation appears to be on another succession track.

This study demonstrated that even short distances from a pool of potential colonists significantly affects the pool of potential colonists. This effect has been observed in habitats as different as glacial forelands (Mathews and Whittaker, 1987), lava flows (Tagawa, 1965), industrial waste heaps (Ash, Gemmell, and Bradshaw, 1994), and vacant lots (Primack and Miao, 1992). Other explanations for the observed patterns, such as inappropriate habitats, physical barriers, or unsuitable germination conditions, do not explain these patterns. The results of this study suggest the following.

1) The dispersal ability of most species is limited. Therefore, dispersal rates may not keep pace with climatic change. Habitat fragmentation may further impede migration. Extinction, reduced habitat diversity and less efficient ecosystems will result. Dominant species may be most prone to this effect if deterministic models developed by Tilman and May (Tilman, 1994, 1997; Tilman et al., 1994) are valid. Human intervention may become necessary to disperse and promote the establishment of most, not just a few, species.

2) Initial species composition, partially determined by stochastic factors due to isolation, can persist. Strong deterministic relationships between environmental factors and species patterns may not develop, thus frustrating analyses of plant–environment relationships.

3) The mass effect (Shmida and Ellner, 1984) predicts that populations near their environmental limits are maintained by chronic recruitment from adjacent populations.

This important effect may be restricted in fragmented landscapes where dispersal barriers accentuate the effects of limited dispersal rates.

Additional questions result from this study. Do biotic processes eventually dominate community structure? If so, is heterogeneity ever fully suppressed? Finally, are early stochastic effects ever fully erased?

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