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Vegetational Heterogeneity along Elevational Gradients

Abstract

How vegetation recovers from disturbance is a central ecological question. We tested the hypothesis that plant spatial heterogeneity declines with increasing functional vegetation age. As pioneers expand and more species invade, we expect heterogeneity to decline. Biomass accumulation and seedling recruitment both drive succession and proceed more slowly at higher elevation. Therefore, we predicted that higher elevation sites would be more heterogeneous than lower sites. We sampled vegetation in five habitats on Mount St. Helens to study recovery 17 years after its most recent eruption. Two lahars were undergoing primary succession and one ridge was recovering from nearly total destruction. A second ridge had been greatly impacted by the blast, while a fifth site was little damaged. Plant cover was analyzed using percentage similarity (PS) and detrended correspondence analysis (DCA). PS decreased with elevation on lahars and on the devastated ridge, but no clear trend was found on less impacted sites. The variation in DCA scores of samples at a site suggested increasing heterogeneity with elevation on one lahar and the strongly disturbed secondary site. The other transects did not show this pattern. These patterns support the hypothesis that heterogeneity declines with increasing successional age. Implicit in the hypothesis is that stochastic factors are important to the establishment of vegetation. High variability among samples of stable vegetation at lower elevation sites suggests that the effects of stochastic establishment can persist.

Introduction

Species assembly during early primary succession is not well understood. Here we compare spatial heterogeneity of vegetation at sites recovering from volcanic impacts on Mount St. Helens. Studies of this volcano suggested that stochastic dispersal (del Moral et al. 1995, del Moral 1998, 1999, Tu et al. 1998) and few safe sites (Tsuyuzaki et al. 1997, del Moral and Grishin 1999) produce initially heterogeneous vegetation. We used a variant of a space-for-time substitution approach to test the hypothesis that spatial heterogeneity declines over time.

The 1980 eruption of Mount St. Helens dramatically altered the surrounding landscape to create a mosaic of impacts (Halpern et al. 1990). A map of impact types appears in del Moral and Bliss (1993). This study describes succession on lahars (mud flows) and recovery on ridges affected to varying degrees. We investigated the hypothesis that vegetation heterogeneity increases with elevation. We assume that an elevation gradient can simulate a temporal gradient. This assumption is based on the fact that high-elevation sites have an effectively shorter history than those at lower elevations because shorter growing seasons and slowed physical amelioration (del Moral and Wood 1993) reduce plant growth and seedling recruitment (Titus and del Moral 1998). Therefore, if stochastic factors dominate early vegetation establishment, then recovering vegetation should be more variable at higher sites than at lower ones.

Materials and Methods

Mount St. Helens (46° 12' N, 112° 11' W) erupted on May 18, 1980. The heat of the eruption melted snow on the cone's east, south, and west sides to spawn lahars that filled valleys and scoured ridges (Foxworthy and Hill 1982). In 1996, 17 growing seasons after the eruption, we sampled vegetation on 1) lahars that are undergoing primary succession, 2) a scoured ridge and a blasted ridge that are experiencing secondary succession (after a partial loss of species), and 3) sites that have fully recovered from minor impacts (cf., Grishin et al. 1996). These sites offered an opportunity to explore how heterogeneity changes during succession.

We studied five transects: Fire Creek, Muddy River, Pine Creek Ridge, Toutle Ridge and Butte Camp. The Fire Creek (900 to 1115 m) and Muddy

River (790 to 1140 m) transects sampled lahars on the east flank of the cone. Both are primary substrates with little organic matter. Surface heterogeneity at each site was similar, and there were no discernible differences in the type or frequency of microsites. The Fire Creek transect was downwind from and near intact vegetation, while the Muddy River transect was upwind and more distant from vegetation (Halpern and Harmon 1983, del Moral 1993). The Pine Creek Ridge (1340 to 1615 m) transect was along a ridge that had been scoured by lahars. Most soil had been removed, but some plants survived (del Moral 1981, 1983; del Moral and Wood 1988). Permanent plots documented that recovery has been gradual and related to elevation. Each sample was on sloping terrain that lacked significant major microsite features. Surface heterogeneity was similar throughout the transect, though the lower clusters had suffered less erosion. Toutle Ridge (1370 to 1615 m) is on the west side of the cone on the edge of the lateral blast. Although trees were killed and some soil was removed, there was substantial survival (del Moral and Wood 1988). High elevation sites were more intensely impacted than lower elevation ones, but surface heterogeneity was similar throughout the transect. Butte Camp (1385 to 1720 m) included three transects on the southwest side of the volcano. These sites experienced only a modest deposit of sandy pumice.

This study was designed to determine the hierarchical nature of spatial heterogeneity. The basic sampling unit was a 1 m^2 *quadrat* within which percent cover was estimated to the nearest 1%. Ten quadrats sampled a circular *plot* with a 10 m radius (314 m^2). Species not sampled, but present, were given cover values of 0.05%. Species within 10 m of the plot, but not in the plot, were given a value of 0.005%. Five plots described a *cluster* and several clusters constituted a *transect*. A transect was started at the center of a plot in representative vegetation while avoiding secondary disturbances such as drainages. The 10 1-m^2 quadrats were placed at 2 and 5 m from the center on the cardinal directions and at 2 m on two additional radii. The four additional plots of a cluster were located 10 to 30 m (randomly determined) in each of the cardinal directions from the center plot.

Heterogeneity was quantified using percentage similarity of cover data (PS) among each sample pair at each level in the hierarchy (among quadrats, among plots and among clusters). PS was calculated using MVSP (Kovach 1993):

$$PS_{ij} = \frac{200\,\Sigma_k\, min\,(X_{ik}, X_{jk})}{\Sigma_k (X_{ik} + X_{jk})}$$

where $\underline{k}$ = the total number of species, X_{ik}, and X_{jk} = the cover of species $\underline{k}$ in each of two samples, $\underline{i}$ and $\underline{j}$, and $\underline{min}$ is the minimum value. Faith et al. (1987) suggested that percentage similarity was a useful measure of species composition. High similarity implies homogeneous samples, while low similarity implies heterogeneity. Spearman rank order correlations (r_s) and linear regressions (r_l) between elevation and similarities were calculated (Analytical Software 1994).

Detrended correspondence analysis (DCA; Hill and Gauch 1980; McCune and Mefford 1997) was used to provide a description of the transects and to assess within-cluster variation. Rare species (frequency < 20% of the most common frequency) were reduced in importance in proportion to their frequency (downweighting). Species that occurred only once were omitted. The arch common to other eigen analyses was eliminated by dividing the first axis into 26 segments and setting the average score on the second axis to zero within each segment. The dispersion of plots within a cluster was determined by the standard deviation of the first DCA axis score along each transect. Each analysis provided an eigenvalue, percent variation on each axis and gradient lengths for comparison.

Results

Sixty-seven species, including conifers, shrubs, forbs, graminoids and mosses, were encountered. There were nearly equal numbers of species at each site: Muddy River, 38 species; Fire Creek, 40 species; Pine Creek, 35 species; Toutle Ridge, 37 species; and Butte Camp, 38 species. Twelve species occurred at every site. Table 1 shows overall cover changes at each site.

The vegetation of the two lahars differed considerably, though both were dominated by rock moss (*Racomitrium canescens*). There were no consistent vegetation patterns at Fire Creek. Cardwell's penstemon (*Penstemon cardwellii*) dominated the middle of the transect, but other species were sporadic. On the Muddy River, dominance shifted from prairie lupine (*Lupinus lepidus*)

TABLE 1. Mean total cover percent of clusters along each transect. Elevations are relative to each transect, starting point adjusted for starting elevation.

	Transect				
Elevation	Muddy River	Fire Creek	Pine Creek Ridge	Toutle Ridge	Butte Camp
Low	111	86			
	75	40			
	48	43			
	16	23	74	41	
	14		77	38	55
Moderate	19		33		49
			31	17	
			20	31	36
			14		17
High			2	8	16

at lower elevations to Cardwell's penstemon and pearly everlasting (*Anaphalis margaritacea*) at higher elevations. Cascade lupine (*L. latifolius*) and subalpine fir (*Abies lasiocarpa*) were dominant at the highest site.

Plant cover at Pine Creek Ridge declined with elevation. Thin bentgrass (*Agrostis diegoensis*) dominated throughout, though its cover was reduced at higher elevations. At lower elevations, several species, including prairie lupine, Cascade lupine, Parry's rush (*Juncus parryi*), Cascade aster (*Aster ledophyllus*) and rock moss, were common. Cover of alpine buckwheat (*Eriogonum pyrolifolium*) and Cardwell's penstemon peaked at mid-elevation.

Toutle Ridge was well vegetated, though cover decreased with elevation. Low elevation plots were dominated by thin bentgrass, Cascade lupine, Cardwell's penstemon, yarrow (*Achillea millefolium*), and rock moss. At mid-and upper-elevations, prairie lupine replaced Cascade lupine, Martindale's lomatium (*Lomatium martindalei*) were common while mosses declined.

Cover declined slightly with elevation at the Butte Camp sites. Grasses declined substantially, but common species such as fleeceflower (*Polygonum newberryi*), alpine buckwheat, and Cardwell's penstemon off-set this reduction with large increases.

Percentage Similarity (PS)

The Muddy River transect spanned 340 m (800 m to 1140 m). The mean PS among the 10 quadrats of a plot declined with increasing elevation from 81.8 to 31.8%. The linear regression was $r_l = -0.97$ ($P < 0.001$), while the Spearman rank correlation (r_s) was -1.00 ($P < 0.03$; Figure 1). The mean similarities of plots within a cluster were higher, but also declined with elevation from 84.5% to 63.5% ($r_l = -0.62$, $P < 0.001$; $r_s = -0.83$ ($P < 0.06$). The overall mean similarity of the six clusters was low 36.5 (8 to 78%), indicating that there was significant variation along this short coenocline.

The Fire Creek transect spanned 210 m (900 to 1110 m). The mean PS of quadrats within a plot declined with increasing elevation from 78.6 to 44.8% ($r_l = -0.81$, $P < 0.001$; $r_s = -1.00$, $P < 0.09$; Figure 2). Cluster mean PS declined with increasing elevation from 83.3 to 58.8% ($r_l = -0.80$, $P < 0.001$; $r_s = -1.00$, $P < 0.09$). The mean similarity between clusters was 56.1 (18 to 86%),

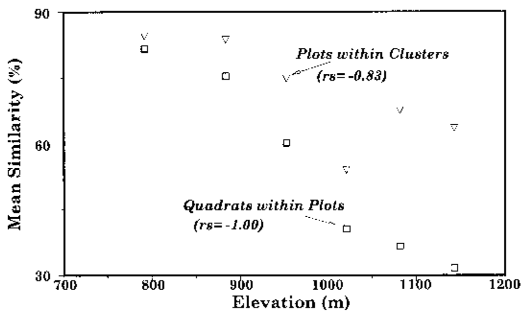

Figure 1. Mean percent similarity of quadrats within plots and plots within clusters on the Muddy River transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was $P < 0.03$; r_s of plots in clusters was significant ($P < 0.06$).

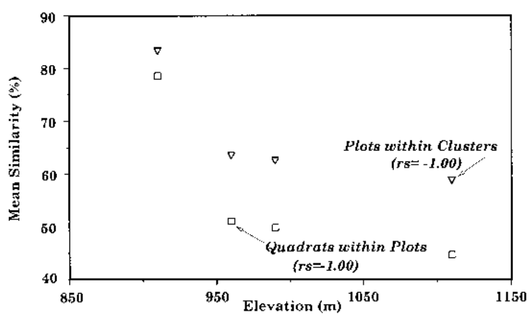

Figure 2. Mean percent similarity of quadrats within plots and plots within clusters on the Fire Creek transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was $P < 0.09$; r_s of plots in clusters was $P < 0.09$).

reflecting greater dominance by mosses and proximity to intact vegetation.

The Pine Creek transect spanned 280 m (1340 and 1620 m). The mean PS of quadrats within a plot declined with elevation from 67.2 to 33.1% (r_l = -0.67, P < 0.001; r_s = -0.71, P < 0.08; Figure 3). Cluster mean PS declined with increasing elevation from 79.4 to 48.9% (r_l = -0.79 (P < 0.001; r_s = -0.78 (P < 0.06). The mean between cluster similarity was 35.8% (1 to 82%) reflecting the steep coenocline and isolation of each cluster.

The Toutle Ridge transect spanned 245 m (1370 to 1615 m). The mean PS of quadrats within a plot varied from 38.6 to 54.8% (Figure 4), with no significant trend (r_l = -0.12, n.s.; r_s = -0.3, P < 0.54). The similarity between plots of a cluster ranged from 51.9 to 73.2%, with no significant elevational trend (r_l = +0.04, n.s.; r_s = 0.40, P < 0.42). The PS between clusters was 38.3 (16 to 59%) indicating that there was significant vegetation change along the coenocline, but that it was not necessarily correlated to elevation.

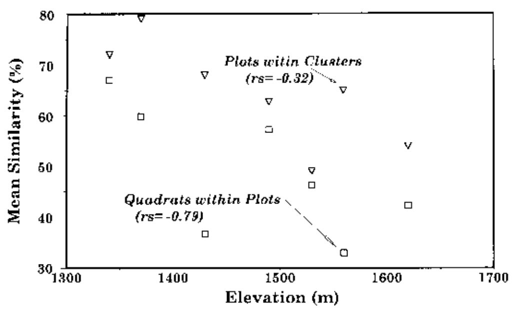

Figure 3. Mean percent similarity of quadrats within plots and plots within clusters on the Pine Creek transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was P < 0.08: r_s of plots in clusters was P < 0.06).

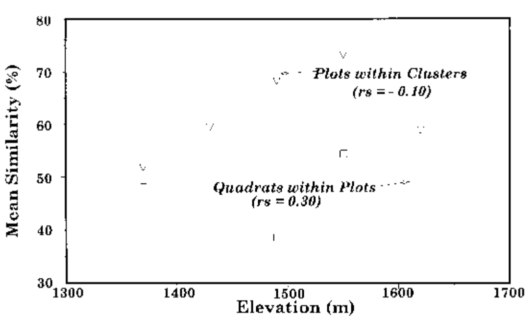

Figure 4. Mean percent similarity of quadrats within plots and plots within clusters on the Toutle Ridge transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was P < 0.30: r_s of plots in clusters was P < 0.42).

The three Butte Camp transects ranged over 200 m (1520 to 1720 m). Mean PS between quadrats of a plot varied from 39.7 to 58.6%, with no significant correlations with elevation. Variation in mean similarity of plots within a cluster varied from 36.2% to 67.6%, with no significant correlations. Mean similarity between clusters was 33.6% (18 to 57%), comparable to other sites. If data from the three transects were combined, there was a significant linear correlation between elevation and within-cluster similarity (r_l = -0.69, P < 0.05). There was no within plot variation trend with elevation in the combined data at Butte Camp.

Detrended Correspondence Analysis (DCA)

DCA provided an alternative way to assess within-cluster variation. Each transect was analyzed independently to determine any significant differences in the structure of the data (Table 2). There were no striking structural differences, but inertia (variance) increased with successional age. Primary surfaces and Pine Creek had low inertia due to strong dominance and low within cluster diversity. The Toutle Ridge and Butte Camp transects had high inertia due to reduced dominance and high within cluster richness. The gradient lengths reflected these differences. The fraction of the explained variance on Axis I was lower for Butte Camp than the primary surfaces because there was greater species richness and equitability at Butte Camp.

TABLE 2. Eigenstructure for each transect analyzed separately.

	Transect				
Parameter	Muddy	Fire	Pine	Toutle	Butte
Eigenvalue I	0.55	0.69	0.48	0.56	0.59
Eigenvalue II	0.22	0.20	0.11	0.30	0.34
Total inertia	1.80	1.60	1.66	2.17	3.62
Gradient Length I	2.69	3.45	3.83	3.19	4.02
Gradient Length II	2.08	1.03	1.70	2.16	2.66
Explained Variance I	30.8	43.5	29.2	25.9	16.4
Explained Variance II	12.2	12.4	6.4	13.6	9.9

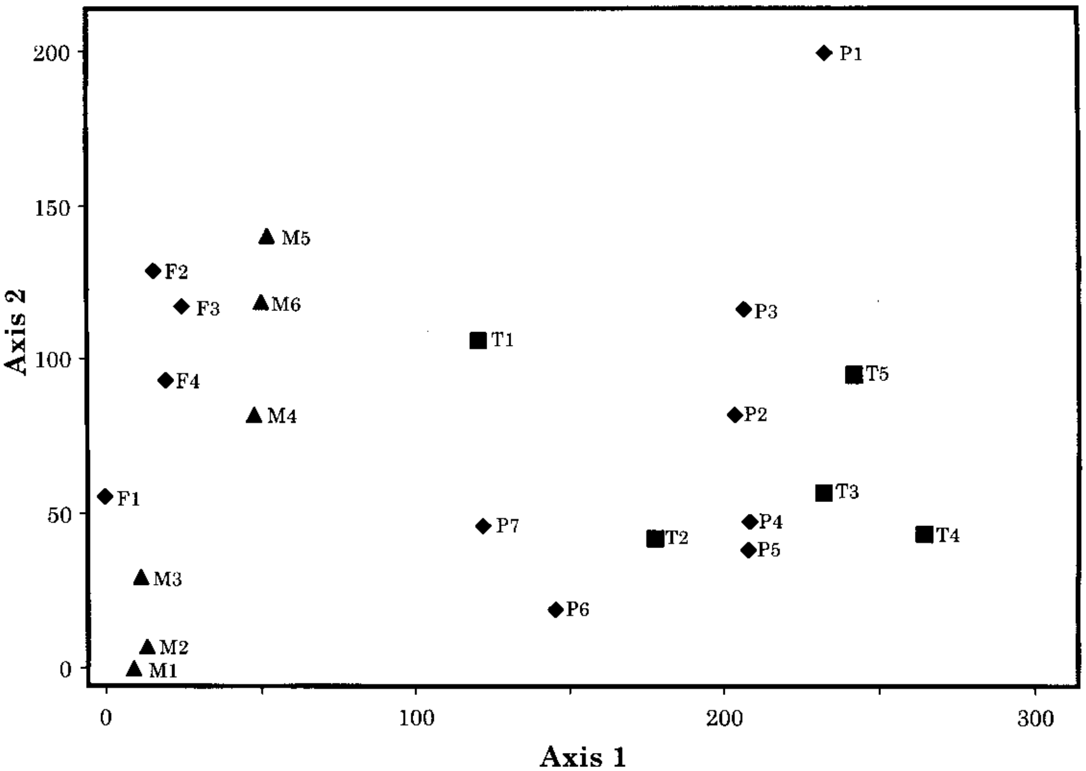

Figure 5. Detrended correspondence analysis of primary successional lahars (M = Muddy River; F = Fire Creek) and a scoured secondary successional ridge (P = Pine Creek Ridge) and a blasted secondary successional ridge (T = Toutle Ridge). Numbers indicate cluster number and increase from low to high elevation for each transect.

Mean cover in each plot of the four successional transects was analyzed to determine transect variation (Figure 5). The lahars (FC and MR) had low Axis I scores, while the secondary sites (TR and PC) had high Axis I scores. Spearman rank correlations (r_s) between elevation and axis scores were determined. The elevation of Muddy River plots increased significantly with both Axis I ($r_s = 0.89$, $P < 0.05$) and Axis II ($r_s = 0.94$, $P < 0.04$). The correlation between Fire Creek elevation and Axis I not significant ($r_s = 0.80$, $P < 0.16$) due to low sample size. The elevation of Pine Creek Ridge plots decreased along Axis I ($r_s = -0.68$, $P < 0.1$) and more strongly along Axis II ($r_s = -0.86$, $P < 0.04$). Toutle Ridge elevation increased along Axis I ($r_s = 0.90$, $P < 0.08$).

A weak pattern of among cluster variation (measured by the standard deviation of Axis I scores) emerged when each transect was analyzed independently (Table 3). There was no trend in the DCA variation on the Muddy River transect.

TABLE 3. Standard deviations of first axis DCA scores of plots within clusters. Each transect was analyzed independently. Elevations are relative to transect.

Elevation	Transects			
	Muddy River	Fire Creek	Pine Creek Ridge	Toutle Ridge
Low	.285	.074		
	.250	.119		
	.092	.040		
	.472	.384	.130	.309
	.145		.152	.509
Moderate	.267		.227	
			.296	.193
			.324	.214
			.279	
High			.318	.472

This may be because this transect was isolated from donor populations and spans a moderate elevation. There was a trend of increased heterogeneity along the elevational gradient on the Fire

TABLE 4. Percent similarity at three scales in four transects. Asterisks indicate significant changes with elevation.

Transect	Elevation Range (m)	Quadrats in Plots	Plots in Clusters	Clusters
Muddy	340	81.8 to 31.8%*	84.5% to 63.5%*	36.5
Fire Creek	210	74.8 to 50.1*	83.3 to 58.8	56.1
Pine Creek	280	67.2 to 33.1*	79.4 to 48.9%*	35.8
Toutle	245	38.6 to 54.8	51.9 to 73.2	38.3

Creek transect. The three lower clusters were near existing vegetation and had received similar influxes of vegetation. The upper site was variable and was the most isolated of the clusters. The Pine Creek Ridge transect showed a trend of increasing heterogeneity with elevation. Though the lowest Pine Creek sites were at higher elevations than the Fire Creek clusters, they were more homogeneous, presumably because they retained a significant residual vegetation. The within-cluster DCA variation on Toutle Ridge was inconsistent, though variation was greater than that of Pine Creek Ridge. Butte Camp variability was high in most cases, but with no apparent trend.

Discussion

Heterogeneity increased with elevation on both lahars and Pine Creek Ridge. Since elevation is related to effective successional time, this result supports the hypothesis that heterogeneity declines during succession. Mean PS declined with elevation among quadrats in a plot and among plots in a cluster. In contrast, we observed no trends at Toutle Ridge or Butte Camp. At these sites, soil and a seed bank survived the eruption and recovery was dominated by residual species that were already well distributed.

A different similarity pattern emerged for vegetation on each transect (Table 4). Within plot similarity has the greatest range on the Muddy River transect, the most isolated transect. Plots within a cluster were relatively homogeneous, due low richness and strong dominance, but clusters differed strongly from one another, in part due to the range of the gradient and in part due to the stochastic nature of invasion patterns. The upper end of this transect was in an early assembly mode while the lower end had begun to fill in gaps by secondary dispersal. The result was that the vegetation of the lower portion was more homogeneous than the upper portion. Lahars on the south side of Mount St. Helens have undergone similar homogenization (del Moral 1998). At Fire Creek, the small elevational range of the transect and its proximity to intact vegetation limited PS changes and resulted in the highest degree of similarity among the clusters. However, heterogeneity did increase significantly with elevation. Pine Creek is developing as if it were a primary successional site. Only a few individuals survived and development has required dispersal from below. Observations made since 1980 suggest that most species have advanced gradually uphill by short distance dispersal. Thus, there is a decline in similarity with elevation at both scales, and between cluster similarity is the least of the four transects. Toutle Ridge had significant surviving vegetation. Despite considerable recovery and colonization since the eruption, there were no trends in similarity over the elevation range sampled. Similarity patterns were not found at Butte Camp.

An alternative method to investigate variation produced ambiguous results. Variation in DCA 1 scores on the Muddy River was inconsistent. The low PS at Cluster 4 corresponds to the high DCA variation at this site, but otherwise there were few points of congruence. In contrast, at Fire Creek and Pine Creek, there were consistent increases in within-cluster variation with elevation that mirrored the patterns exhibited by PS data. DCA also did not demonstrate a trend on Toutle Ridge. DCA demonstrated progressive changes among plots on each transect. Such trends are usually interpreted as the results of elevation. Here, we suggest that different relative successional stages could contribute to the observed regularities in DCA scores.

The large between cluster heterogeneity on the Toutle transect and at Butte Camp suggests that stochastic factors may not dominate only early in primary succession and then disappear due to deterministic factors such as competition. Chance may control patterns along a continuous gradient that parallel patterns caused by disturbance.

Stochastic factors appear to be a strong force in primary successional sites, but those factors are masked when species survive in more moderately impacted sites. Elements of stochastic initiation of vegetation may never be obliterated and must be considered in the analysis of vegetation pattern (Lavorel and Lebreton 1992, del Moral et al. 1995). Though certain life-history traits may be favored on particular substrates (Tsuyuzaki and del Moral 1995), species composition is affected by landscape factors that produce initially heterogeneous vegetation.

In this study we demonstrated that less mature vegetation was more variable than more mature vegetation. We used elevation as a surrogate for relative successional time. As habitat variability did not change perceptibly along any transect, we are confident that factors related to elevation, not habitat heterogeneity, are responsible for the observed vegetation responses. Similar trends of declining heterogeneity should be expected in long-term chronosequence studies and in the comparison of sites at which other factors contribute to a gradient of different effective developmental age.

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