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Local species turnover on Mount St. Helens, Washington

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Abstract. The 1980 eruption of Mount St. Helens provided a chance to study species turnover during succession. I used permanent plots to monitor species presence in 0.25-m^2 quadrats. Colonization and extinction were estimated for three several-year increments in 10 habitats starting seven seasons after the eruption by two methods. Extinction rates, measured by the proportions of initially filled quadrats that lost a species, varied little across sites. Extinction percentages, the proportion of all quadrats losing a species, declined from recovered to secondary to primary sites. Extinction percentages increased through time on successional sites. Colonization rates and percentages were similar on all sites. The proportion of extinction percentage to colonization percentage declined from recovered sites, where these processes were of similar magnitude, to primary sites, where the ratio was about 1 to 4. These results suggest that the carousel model is operative even during community assembly.

Keywords: Carousel model; Local colonization; Local extinction; Primary succession; Secondary succession; Volcano.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

The lateral eruption of Mount St. Helens on 18 May 1980 removed the north half of its cone. The blast seared ridges. Subsequent pyroclastic flows, pumice deposits and lahars created a new landscape. The south slope was impacted by tephra. Starting in 1980, I established permanent plots to monitor vegetation establishment and recovery. This paper describes species turnover (colonization and extinction) in permanent quadrats on new surfaces (primary succession), intensely impacted sites (secondary succession) and recovered sites (tephra).

Study area

Mount St. Helens is centered at 46° 20' N, 122° 18' W, with an elevation of 2549 m. This study used 10 sets of permanent plots that represent unique combinations of impact intensity. Del Moral & Bliss (1993) provided a map and detailed descriptions of these sites.

Recovered sites were impacted by air-fall deposits of coarse pumice (tephra) that buried vegetation on the southern slopes of the cone up to 20 cm. The coarse texture, shallow depth and subsequent erosion permitted significant survival and rapid recovery (del Moral 1983).

Secondary succession sites received a variety of impacts. Blast A is on the west side of the cone, at the edge of the directed blast. The blast killed woody plants, but some dormant herbaceous vegetation survived. Rapid snow-melt formed lahars (mud-flows) that scoured canyons and ridges before forming deposits at lower elevations. Two ridges were scoured on the east side of the volcano. Scour A is within 100 m of surviving herbaceous vegetation, while Scour B is more isolated. Scour C is on the south side of the volcano.

Three primary succession habitats were sampled. Lahars formed on meadows on the south side of the cone (del Moral 1998). Proximity to intact vegetation permitted rapid establishment. Blast B, on the northwest cone, was destroyed by the lateral blast (del Moral 1993). The Pumice site on the north side was seared by the lateral blast and covered by pumice (del Moral et al. 1995; del Moral & Wood 1993).

Methods

Each plot is permanently marked to permit accurate repeated sampling. Species presence and cover were recorded at 1-m intervals on four radii (n = 24). From 1986 to the present, 0.25-m^2 quadrats have been used.

Colonization and extinction were calculated from 0.25-m^2 quadrats during three intervals. In most cases, comparisons were from 1986 to 1991, 1989 to 1994 and 1991 to 1997. Blast A sites were not sampled from 1988 to 1993, so comparisons were from 1986 to 1994, 1987 to 1995 and 1994 to 1997. Pumice sampling started in 1989, so comparisons were from 1989 to 1992, 1991 to 1995, and 1992 to 1997.

The extinction rate of a species is the fraction of quadrats occupied at T_0 that are empty at T_1. The colonization rate is the fraction of initially empty quadrats that are occupied at T_1 (Fröborg & Eriksson 1997). Empty quadrats usually greatly outnumbered filled ones, so the same number of events produces a higher extinction rate than a colonization rate. Therefore, the extinction and colonization rates were also calculated as a percentage of the total number of quadrats.

Trends were summarized in recovered, secondary and primary sites. At each site, for each yearly comparison, the percent colonization and extinction were compared. If one was at least twice the other, it was so scored and the total score converted to an index from –1 to +1. For example, there are six possible comparisons on recovered sites. If a species had predominant extinction on 1, no difference on 2, and predominant colonization on 3 of the comparisons, the index would be equal to 3 colonizations less the 1 extinction/6 comparisons, or +0.33.

Results

Extinction and colonization rates

Extinction and colonization rates were calculated for species with at least four occurrences (Table 1) and the means determined for each habitat. Extinction rates during the three intervals showed no strong pattern on recovered sites. On secondary sites, they increased slightly. On primary sites, they generally increased, as cover developed. These values are unstable because several species were infrequent and short lived (e.g. *Epilobium angustifolium*, *Lupinus lepidus* and *Hypochaeris radicata*).

Colonization rates were usually lower than the comparable extinction rates because there were more quadrats to be colonized for most species in any year. There were no trends on either recovered or secondary sites. On primary sites colonization rates may be increasing.

Extinction and colonization percentages

Extinction and colonization rates cannot be compared directly among sites or intervals because they are affected by sample sizes. Though imperfect, a better view of between- and within-site trends is provided by the percentage of all quadrats that changed during an interval (Table 2).

There were always more colonizations than extinctions at successional sites, while no pattern emerged on recovered sites. Extinction percentages were high on tephra (4.6 to 12.3% of total quadrats), moderate on secondary sites (1.2 to 4.9% of quadrats) and low on primary sites (0.6 to 5.2%). Colonization rates were relatively high in all cases and demonstrated no pattern between sites. Tephra sites varied from 3.9 to 17.0% of the quadrats, secondary sites varied from 5.8 to 15.3% of the quadrats, and primary sites varied from 3.9 to 15.9% of the quadrats. The disparity between these two processes is reflected by the ratio of extinctions to colonizations. These ratios approach 0.9 on recovered sites, vary from 0.26 to 0.45 on secondary sites and from 0.19 to 0.26 on primary sites.

Individual species patterns support the statistical summaries (Table 3). Species on recovered sites showed low index scores, indicating no trend of either colonization or extinction. Secondary and primary site scores were all positive, some strongly so. Most individual species colonized more often than they became locally extinct.

Discussion

The concept of local species turnover is embedded in recent studies of vegetation dynamics (Hanski 1982; Lavorel & Lebreton 1992; Collins et al. 1993; Hoagland & Collins 1997). The rate of turnover at small scales in stable meadows is high (van der Maarel & Sykes 1993; Herben et al. 1997). Fröborg & Eriksson (1997) showed that local colonization and extinction rates in a stable forest understory at a scale of 100 m^2 over a 20-yr interval were relatively high. Van der Maarel et al. (1995) suggested that there was little evidence for niche structure on a small scale, indirectly supporting a carousel model. Van der Maarel & Sykes (1997) quantified the rate of local mobility among species and found it much larger than generally recognized.

The present study shows that species are locally mobile. It differs from previous studies of local turnover in that it explores an intermediate scale and it investigates the process against a successional background. Species present in 1986 may have survived the 1980 impacts, arrived by long-distance dispersal or grown into the quadrat. Once present, a plant may be lost by senescence (e.g. *Lupinus lepidus*, *Hypochaeris radicata* and *Hieracium gracile*), grazing (e.g. *Aster ledophyllus* and *Castilleja miniata*), die-back (e.g. *Penstemon cardwellii* and *Polygonum newberryi*), or competitive displacement from species such as *Agrostis diegoensis*.

Extinction rates in recovered, secondary and primary sites were similar and generally high. The highest rates

Table 1. Mean extinction and colonization rates on Mount St. Helens. The extinction rate is the fraction of quadrats that contained the species in the first year but lost that species by the next comparison year. The colonization rate is that fraction of empty quadrats in the base year that acquired that species by the next comparison.

	Recovered sites			Secondary sites				Primary sites		
	Tephra A	Tephra B	Tephra C	Scour A	Blast A	Scour B	Scour C	Lahar	Blast B	Pumice
Extinction Rate I	.36	.36	.20	.11	.24	.26	.24	.32	.03	.44
Extinction Rate II	.52	.34	.25	.16	.30	.26	.18	.08	.30	.35
Extinction Rate III	.37	.33	.29	.17	.29	.28	.33	.66	.39	.71
Colonization Rate I	.32	.10	.09	.06	.26	.16	.07	.08	.07	.04
Colonization Rate II	.20	.07	.11	.16	.23	.13	.07	.14	.16	.07
Colonization Rate III	.14	.12	.15	.09	.17	.14	.12	.11	.18	.11

Table 2. Mean extinction and colonization percentages on Mount St. Helens, calculated as the fraction of the total number of quadrats that were affected. The extinction to percent ratio was calculated from the mean rates.

	Recovered sites			Secondary sites				Primary sites		
	Tephra A	Tephra B	Tephra C	Scour A	Blast A	Scour B	Scour C	Lahar	Blast B	Pumice
Extinction % I	5.3	4.7	4.6	2.6	1.8	2.5	2.0	0.9	1.8	0.7
Extinction & II	12.3	6.3	4.8	2.8	4.9	3.3	1.2	0.9	0.6	1.5
Extinction % III	9.1	6.8	6.5	3.7	4.7	4.7	2.5	5.2	4.7	1.8
Mean Extinction Percent	**8.9**	**5.9**	**5.3**	**3.0**	**3.8**	**3.5**	**1.9**	**2.3**	**2.3**	**1.3**
Colonization % I	17.0	6.5	6.2	5.8	13.2	12.0	5.8	6.2	13.2	3.9
Colonization % II	6.1	3.9	7.1	7.6	15.3	8.3	6.8	12.4	15.9	6.1
Colonization % III	6.2	10.3	9.3	6.8	6.5	8.7	9.5	7.9	6.5	6.7
Mean Colonization Percent	**9.8**	**6.9**	**7.5**	**6.7**	**11.7**	**9.7**	**7.4**	**8.8**	**11.9**	**5.6**
Extinction/Colonization ratio	**0.91**	**0.86**	**0.71**	**0.45**	**0.32**	**0.36**	**0.26**	**0.26**	**0.19**	**0.23**

Table 3. Net extinction and colonization of representative species in each successional category. Values range from – 1.0 to +1.0 (see Text). Blanks indicate species absent or rare.

Species	Recovered	Secondary	Primary
Abies lasiocarpa			0.33
Agrostis diegoensis	0.5	0.88	0.67
Anaphalis margaritacea			0.5
Aster diegoensis	– 0.33	0.12	
Carex mertensii		0.38	0.33
C. rossii	0.16		
Eriogonum pyrolifolium	– 0.33	0.75	0.16
Hieracium albiflorum		0.25	0.33
H. gracile		0.25	
Hypochaeris radicata			0.67
Juncus parryi	0.16	0.75	0.33
Lomatium martindalei	0.0	0.25	0.16
Luetkea pectinata	0.0	0.5	0.33
Lupinus lepidus	0.0	0.25	0.67
Penstemon cardwellii		0.63	0.83
Pinus contorta			0.33
Polygonum newberryi	0.33	0.25	0.16
Spraguea umbellata		0.5	0.33
Stipa occidentalis		0.63	0.16

occurred on primary surfaces during the last increment. The development of these primary successional sites masks these high extinction rates. The extinction percentage declined from recovered to primary sites because there were far fewer quadrats with species at risk in primary sites than in stable ones. However, as successional sites developed, the extinction percent increased substantially.

The colonization rate was high, even on recovered sites. Empty plots are colonized at similar rates on all sites, provided neighbors are present. Colonization percentages, expressed as a percentage of all quadrats, are similar on all surfaces. This implies that population dynamics are similar on all sites. The ratio of extinction to colonization percentages provides a good basis for comparison. In recovered sites, extinction events are nearly as frequent as colonization events, varying largely with summer moisture conditions. In secondary sites, extinction events are one third as common as colonization events. On primary sites colonization events are more than four times more common than extinction events.

Small-scale extinctions and colonizations are based on individual life histories, dispersal ability and proximity to seed sources. Some deterministic extinction may have occurred in well-vegetated plots, but rates were also high in open plots. Colonization rates were no lower in recovered sites than the others, suggesting that the presence of moderately dense vegetation does not inhibit invasion. Stochastic extinction and colonization appear to dominate local population dynamics of successional sites. While successional status affected these rates, each habitat is dynamic. Species appear and disappear in ways consistent with the carousel model. The species in these habitats do not have narrow, discrete niches. Therefore, they may coexist in small samples or they may replace one another in a non-deterministic way.

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