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Vegetation changes in blown-down and scorched forests 10–26 years after the eruption of Mount St. Helens, Washington, USA

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Abstract We examine patterns of vegetative change in blown-down and scorched forests in the blast zone of Mount St. Helens (USA), 10–26 years after the eruption. We compare trends in community attributes in four post-eruption environments, or site types, defined by severity of disturbance, presence/absence of a protective snowpack at the time of eruption, and seral state (previously clearcut vs. mature/old forests). Permanent plots established in 1980 at 16 sites were sampled at 5- to 6-year intervals between 1989 and 2005. Data on species presence and abundance were used to characterize changes in total plant cover, life-form spectra, species diversity, species turnover, and community composition. Due to the magnitude and heterogeneity of disturbance, vegetation re-establishment was gradual and highly variable among sites. Total plant cover averaged 36–70% after 26 years. Early-seral forbs were dominant except in snow-protected sites, where surviving shrubs were most common. Tree regeneration remained sparse after 26 years (< 6% cover in all but two sites). Species richness increased in all site types, reflecting greater species gain than loss, although rates of gain declined with time. Species heterogeneity, integrating the number and abundance of taxa, did not increase. Successional trajectories were distinct, but parallel among sites, reflecting legacies of pre-eruption composition, variation in disturbance severity, and differences in composition of early-seral colonists. Slow re-colonization by forest herbs and trees likely reflects seed limitations and abiotic stress rather than competition from early-seral species. Succession following this major eruption is both slow and contingent on pre-conditions, nuances of the disturbance, and species' life histories.

Keywords Succession · Species diversity · Species turnover · Vegetation dynamics

Introduction

Disturbance is fundamental to vegetation change. It is universal (at some temporal scale); causes mortality, resetting the competitive hierarchy among species; alters the physical environment within which species

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colonize or interact; and ultimately, redirects succession (Sousa 1984; Glenn-Lewin and van der Maarel 1992; Attiwill 1994; Peet et al. 2014). Natural disturbances vary in size, frequency, intensity, timing, and duration, and each of these characteristics can affect vegetation change independently or jointly (Sousa 1984; Turner et al. 1998). Large, infrequent disturbances (LIDs; Foster et al. 1998; Turner et al. 1998) are characteristic of many temperate and boreal ecosystems. LIDs are critical determinants of future vegetation and ecosystem function because they affect large areas, modify abiotic conditions, cause high (albeit variable) levels of mortality, and set in motion trajectories of vegetation change that can play out over centuries (Foster et al. 1998; Turner et al. 1998).

By virtue of their size, LIDs are characterized by spatial heterogeneity in initial disturbance effects, including variation in the survival of seeds and vegetative propagules, and in the physical environments in which species colonize and interact (Adams et al. 1987; Foster et al. 1998; Turner et al. 1998; Wang and Kemball 2005). As a consequence, LIDs can initiate multiple trajectories of vegetation change characterized by varying rates or patterns of biomass accumulation, life-form development, and species turnover (Halpern and Franklin 1990; Foster et al. 1998; Turner et al. 1998; Wang and Kemball 2005). Although plant cover and diversity are often reduced to low levels by LIDs (Turner et al. 1998; Halpern et al. 1990), rates and patterns of recovery can vary greatly (Stickney 1986; Halpern and Franklin 1990; del Moral 2000, 2007; Romme et al. 2016). For example, in forests of the Pacific Northwest, the typical progression of post-fire dominance is from annual to perennial herbs, then to taller shrubs and trees (Schoonmaker and McKee 1988; Halpern and Franklin 1990; Yang et al. 2005). However, in some circumstances, the period of herb or shrub dominance may be greatly extended, delaying or preventing development of closed-canopy forest (Stickney 1986; Halpern and Franklin 1990; Donato et al. 2012).

The LID framework is useful for examining vegetation recovery following volcanic eruptions. This framework, and disturbance theory more generally, suggests that post-eruption changes can be a complex consequence of pre-existing vegetation, disturbance effects, landscape context, and chance (Foster et al. 1998; Turner et al. 1998). Due to variation in disturbance severity or in the depth and physical properties of volcanic deposits, reassembly may occur through a combination of primary and secondary successional processes, i.e., colonization of new substrates or re-emergence of surviving plants (Grishin et al. 1996; Turner et al. 1998; del Moral 2000). The pace and pattern of vegetation change during succession depend on the fundamental processes of species' gain and loss (Myster and Pickett 1994; Anderson 2007). Although rates of gain generally decline over time (Anderson 2007), spatial and temporal variation in rates of gain or loss, and in the traits of species that contribute to these trends, offers insights into the underlying mechanisms of vegetation change (e.g., abiotic constraints, dispersal limitation, and competition).

In May 1980, Mount St. Helens erupted cataclysmically, creating a large and heterogeneous landscape of disturbed habitats, including ~ 500 km^2 of 'blown-down' and 'scorched' forests (Adams et al. 1987; Turner et al. 1997; Dale et al. 2005b). In blown-down forests (370 km^2), trees were leveled by the force of the blast. In scorched forests at the perimeter of the blast zone (110 km^2), wind speeds and temperatures were lower. Here, trees were killed but left standing, with fine branches and foliage scorched by the heat of the blast (Dale et al. 2005a). In addition to these mechanical and heating disturbances, tephra (ash and pumice) from the initial and secondary eruptions was deposited to depths of 10–60 cm (Waitt and Dzurisin 1981). Although the lateral (horizontally directed) blast may be a unique feature of the 1980 eruption, Mt. St. Helens has erupted numerous times in the past 4000 years, generating comparably deep deposits of tephra in 1480 and 1800, and more frequent, shallower deposits in between these events (Waitt and Dzurisin 1981; Mullineaux 1986).

In this paper, we build on early studies of succession in this landscape (Means et al. 1982; McKee et al. 1987; Franklin et al. 1985; Halpern et al. 1990), exploring variation in plant community development two and three decades after the eruption. We assess trends within and among 'site types'—a post-eruption classification of the landscape that incorporated factors likely to influence vegetation recovery: disturbance severity, presence of snowpack at the time of the eruption, and pre-disturbance seral state. Four site types were defined: 'blown-down forests' (high-severity disturbance with complete loss of overstory and near-complete loss of understory); 'blown-down forests with snow' (similar, but with understories protected by snowpack); 'scorched forests' (less severe disturbance with significant but not complete loss of understory); and 'clearcuts' (forested areas cut before the eruption and dominated by early-seral species). Studies of the first decade of succession highlighted the following trends (Halpern et al. 1990): (1) slow but significant increases in species richness and cover (to ~ 10%), with few differences among site types; (2) widespread dominance by perennial (mostly early-seral) forbs; (3) greater abundance of surviving shrubs in snow-protected sites; (4) distinct compositional trajectories among site types, with increasing similarity of blown-down and scorched forests to clearcuts (the primary seed source for early-seral forbs). Here we examine vegetation changes within and among site types, 10–26 years after the eruption. We compare trends in plant cover, life-form dominance, species diversity, species turnover (gain and loss), and community composition. Drawing from early observations (Halpern et al. 1990) and successional theory, we hypothesized the following:

H1 Plant cover will continue to increase in all site types, reaching greatest levels in sites protected by snow at the time of the eruption.

H2 Forbs, which dominated much of the early post-eruption landscape, will decline in relative abundance as shrubs increase; shrubs will continue to dominate in blown-down forests with snow, where their initial survival was highest.

H3 Species richness will continue to increase, but heterogeneity (incorporating the richness and abundance of species) will not, as species' evenness declines. Richness will peak earlier in snow-protected sites (initially richer in forest species) and later in clearcuts (initially poorer in species).

H4 Consistent with trends in richness, rates of species' gain will exceed rates of loss. However, rates of gain will decline with time, reducing turnover. Gains will be lowest in snow-protected sites where initial survival was greatest.

H5 Blown-down and scorched forests will retain distinct species' compositions (legacies of pre-eruption composition and disturbance severity), but will diverge from clearcuts, as early-seral dominants are replaced by closed-forest species.

Methods

Study area

Study sites established in 1980 are within or adjacent to the Mount St. Helens National Volcanic Monument (46°16′N, 122°09′W) in the southern Cascade Mountains of Washington. Sites fall within the *Tsuga heterophylla* and *Abies amabilis* forest zones (Franklin and Dyrness 1973). Prior to the eruption, forests included old-growth, mature, and second-growth stands, as well as clearcut and replanted forests. The climate is characterized by cool, wet winters (average minimum temperature in January of − 4.4 °C) and warm, dry summers (average maximum temperature in July of 22.3 °C). Annual precipitation is 237 cm, but highly seasonal, with < 10% falling during the summer months (Swanson et al. 2005). At higher elevations (*Abies amabilis* zone) winter snowpack may persist into early summer.

Site types, site selection, and sampling design

The original design included 35 sites stratified by site type (Means et al. 1982). Where possible, sites representing different site types were established in pairs or triplets to block for environmental or compositional variation. Of the initial sites, 16 were sampled consistently between 1989 and 2005 and form the bases of the current analyses. Replication of site types ranges from 3 to 6 (Table 1). Sites capture the major physical environments and disturbance effects found within the blown-down and scorched zones (Table 1). Elevations range from 710 to 1250 m, slopes are flat to steep (0–63%), and aspects vary. Distance to the crater ranges from 11.4 to 17.9 km and initial tephra depth ranged from 9 to 46 cm (Table 1). Site types were defined as follows:

1. *Blown-down forests (BD)* Nearly all trees were uprooted or snapped within 10 m of the ground; most above-ground parts of understory plants were destroyed.
2. *Blown-down forests with snow (BDS)* Similar disturbance to trees as in BD, but due to elevation and aspect, there was a spring snowpack, protecting understory shrubs and small trees.
3. *Scorched forests (S)* Trees remained standing (with scorched foliage) in a narrow band at the

Table 1 Locations, site types, and physical characteristics of the 16 study sites

Location	Site type[a]	Distance from crater (km)	Slope (%)	Aspect (deg)	Elevation (m)	1980 tephra depth (cm)
Cedar Creek	BDS	11.4	40	90	1250	33
Cedar Creek	CC	11.4	5	90	1250	46
Commonwealth Mine	BD	15.3	63	226	1100	12
Commonwealth Mine	S	15.3	60	220	1100	12
Commonwealth Mine	CC	15.3	50	234	1100	16
Meta Lake (N)	BDS	13.6	32	180	1100	9
Meta Lake (S)	BDS	13.6	32	14	1100	16
Meta Creek	CC	13.6	5	0	1100	24
Middle Clearwater Creek	S	15.8	8	249	710	20
Middle Clearwater Creek	CC	15.8	3	198	710	21
Polar Star Mine	S	17.9	0	—	850	13
Upper Bean Creek	BD	12.4	49	117	1150	36
Upper Bean Creek	CC	12.4	46	91	1150	24
Upper Clearwater Bridge	BD	14.8	7	56	750	25
Upper Clearwater Bridge	CC	14.8	25	39	750	15
Upper Green River	BD	17.0	0	—	880	21

[a] Site types: *BD* blown-down forest, *BDS* blown-down forest with snow, *S* scorched forest, *CC* clearcut

edge of the blow-down zone. Most, but not all, above-ground parts of understory plants were destroyed.

4. *Clearcuts (CC)* Similar disturbance severity as BD, but with young (< 13 years) post-harvest plantations dominated by early-seral species.

Each site was sampled with three, circular, 250 m^2 (8.92 m radius) plots spaced 50 m apart. Sampling occurred at 5- to 6-year intervals over the study period: 1989 (year 10), 1994, 2000, and 2005 (year 26). Cover of each vascular plant species was estimated to the nearest 0.001 m^2, converted to percent (%), and averaged for the three plots in each site. Plants that could not be identified to species were recorded at the genus level. A small number of unidentified seedlings were excluded from the analyses. Nomenclature follows Hitchcock and Cronquist (1973).

Response variables

Our hypotheses address variation in the following community attributes: total plant cover ($H1$), relative cover of dominant life forms ($H2$), components of diversity ($H3$), species turnover (gain and loss) ($H4$), and composition ($H5$). For each site × sampling date, total plant cover was computed as the summed cover of individual species. Plant species were assigned to one of five life forms: sedge/rush, grass, forb (including ferns), shrub (multi-stemmed woody species), or tree (see Online Resource 1). Cover was summed for species within each life form; relative cover was computed as the proportion of total cover. We computed three indices or components of diversity: richness, heterogeneity (sensu Peet 1974; integrating the number and relative abundance of species), and evenness (equitability of species' abundance). For ease of interpretation and comparability to previous analyses, we used the Hill indices and ratios (Hill 1973; Peet 1974). Richness (N_0) was computed at two spatial scales: mean number of species per plot (250 m^2) and number of species per site (750 m^2). Heterogeneity (N_2) was computed for each site as the reciprocal of Simpson's index, $1/\Sigma p_i^2$ (where p_i is the proportional abundance of species i). Heterogeneity shares the same units as richness and can be expressed as the number of equally common species required to produce the same diversity as that in the observed sample (Peet 1974). Evenness, R_1, was computed as the ratio of N_2 and N_1, (where N_1 is the exponent of Shannon's information measure, $\exp - [p_i \times \log p_i]$). Finally, species gain (colonization), loss (local extirpation), and turnover (average of gain and loss) were computed for each site as proportions, based on species' presence/absence at the start and end of each sampling interval (Anderson 2007).

Species were classified by seral status (early-seral, closed-forest, or non-forest; see Online Resource 1) to aid in interpretation of trends in cover and richness. Species assignments followed previous studies (Halpern and Franklin 1990; Halpern et al. 1990, 2012) or descriptions in the regional flora (Hitchcock et al. 1969). Non-forest species were characteristic of undisturbed openings (meadows, barrens, or wetlands). Cover was summed and richness was tallied for species within each group from which relative cover and richness were computed.

Statistical analyses

We used repeated measures PERMANOVA (Anderson 2001) to assess variation attributable to site type, time, and their interaction (fixed effects). Site (nested within site type) was treated as a random effect. Separate models were run for total plant cover; relative cover of forbs and shrubs; richness, heterogeneity, and evenness; and rates of gain, loss, and turnover. Cover variables were square-root transformed before analysis. Euclidean distance was used as the distance measure. Analyses were implemented in PRIMER ver. 6 (Clarke and Gorley 2006). Significant effects of site type or of site type × time were followed by pairwise comparisons of site types or of site-types within years, respectively.

We used regression analyses to explore temporal trends when PERMANOVA indicated a significant effect of time. Separate regressions were run for each site type (n = 12 to 24 sites × sampling dates). Where scatterplots suggested non-linear relationships (accelerating or peaking over time) we compared linear to non-linear models, choosing the 'best fit' model as that with the highest adjusted R^2 (Halpern and Lutz 2013). Cover data were square-root transformed before analysis.

To assess compositional changes, we used nonmetric multi-dimensional scaling (NMS, Kruskal 1964). The species × sample matrix contained the mean cover of species in each site × sampling date (n = 64). Infrequent species (present in $< 5\%$ of samples) were excluded and cover was arcsine square-root transformed. NMS was implemented in PC-ORD ver. 6.0 (McCune and Mefford 2006) using the 'slow and thorough' autopilot setting, Bray–Curtis as the distance measure, a random start, a maximum of 500 iterations (250 runs with real and randomized data), and an instability criterion of 1×10^{-7} (McCune and Grace 2002). A scree plot of stress versus dimensionality suggested a three-dimensional solution with a stress of 12.0. We displayed results graphically in two ways: as trajectories of individual sites and site types (means of 3–6 sites).

Results

Total plant cover (*H1*)

As predicted, total plant cover increased continuously in most site types (Fig. 1a). In blown-down forests (BD), however, it declined in the last interval. Accordingly, the temporal trend in BD was best modeled as 'peaking' (Table 2). For blown-down forests with snow (BDS) and clearcuts (CC) the best models were linear, although the variation explained was small ($R^2 < 0.25$; Table 2). For scorched forests (S), linear and 'accelerating' (logarithmic) models were comparable (R^2 = 0.42–0.43; Table 2). Despite the general increase in cover in all site types, individual sites within most types showed idiosyncratic declines at various points in time resulting in significant variation within site types (Fig. 1a). Although we predicted greatest cover in snow-protected sites (BDS), differences in cover among site types were limited to year 21 (BDS and BD > CC; Fig. 1a).

Relative abundance and seral composition of life forms (*H2*)

We predicted that where forbs had dominated the early post-eruption period (all site types except BDS), they would gradually be replaced by shrubs. Trends in relative cover supported this prediction in most, but

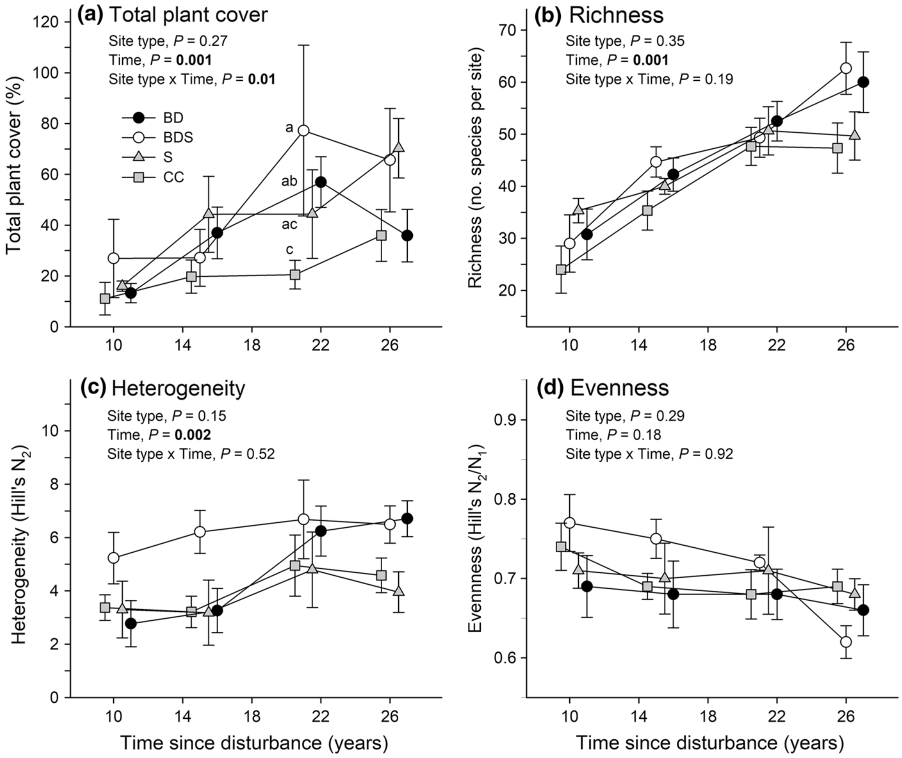


Fig. 1 Temporal trends in **a** total plant cover, **b** richness (species per 750 m^2), **c** heterogeneity, and **d** evenness. Values are means of 3–6 sites (± 1 SE); site types are offset on the *X* axis to reduce overlap. *P* values are from PERMANOVA; bold font indicates a significant effect ($P \leq 0.05$). In post hoc comparisons of total plant cover among site types within years, the only significant differences were in year 21 (BDS and BD > CC). Site-type codes are defined in Table 1

not all BD and S sites (Fig. 2; Online Resource 2). Trees remained sparse (< 6% cover) at all but two sites. In one S site, the notable exception, cover of *Pseudotsuga menziesii* and *Tsuga heterophylla* (47%) greatly exceed that of shrubs (28%) (Online Resource 2). In CC, shrubs remained distinctly under-represented (significant site-type effect, Fig. 2).

Early-seral species accounted for most forb cover (Fig. 3). However, the seral composition of shrubs varied markedly among sites and site types. In S, residual forest species (*Acer circinatum*, *Rubus ursinus,* and *Vaccinium ovalifolium*; Online Resource 2) dominated the shrub layer (92–97% of shrub cover). In BD, the seral composition of shrubs varied among sites (Online Resource 2). In BDS, early invasion and clonal expansion of *Alnus sinuata* shifted dominance from surviving (*Vaccinium membranaceum* and *V. ovalifolium*) to an early-seral shrub (Fig. 3).

Species diversity (*H*3)

In total, 206 species were recorded over the study. Totals increased from 124 (in year 10) to 144 (year 15), 158 (year 21), and 173 species (year 26) (Online Resource 1). As predicted, species richness increased in all site types (Fig. 1b; Table 2), with site-scale richness nearly doubling over the sampling period (Fig. 1b). Plot-scale trends were very similar, but less steep (data not shown). At 10 years, sites had 18 more species on average than did individual plots; after 26 years, the difference was ~ 25 species. Although richness appeared to plateau after 21 years in S and CC, temporal trends were best modeled as linear (Table 2). Counter to expectation, richness did not peak earlier in BDS (richer post-eruption flora) than in CC (depauperate flora) (Fig. 1b; Table 2).

Forbs were consistently the most diverse life form. Shrub species were notably lacking in CC (Fig. 4). Early-seral species were more diverse than forest species in all site types except BDS (Fig. 5). Relative

Table 2 Results of regression models of temporal trends in total plant cover, richness, heterogeneity, and evenness

Response variable/Site type	Model form (terms)	β_1	β_2	Adj. R^2	P
Total plant cover[a]					
Blown-down forest[b]	Peaking (x, x^2)	0.146	− 0.004	0.43	**0.010**
Blown-down forest with snow[c]		0.024		0.24	0.06
Scorched forest[b]	Accelerating (log x)	0.921		0.42	**0.014**
Clearcut		0.017		0.23	**0.010**
Richness (species/site)					
Blown-down forest		1.82		0.63	**0.001**
Blown-down forest with snow		1.93		0.72	**0.001**
Scorched forest[c]		0.94		0.45	**0.011**
Clearcut[c]		1.61		0.47	**0.001**
Richness (species/plot)					
Blown-down forest		1.19		0.71	**< 0.001**
Blown-down forest with snow		1.40		0.63	**0.001**
Scorched forest[c]		0.79		0.53	**0.004**
Clearcut[c]		0.99		0.39	**0.001**
Heterogeneity (Hill's N_2)					
Blown-down forest		0.286		0.54	**0.001**
Blown-down forest with snow		—		0.07	0.21
Scorched forest		—		0.04	0.45
Clearcut[c]		—		0.07	0.11
Evenness (Hill's N_2/N_1)					
Blown-down forest		—		0.04	0.53
Blown-down forest with snow		− 0.06		0.39	**0.018**
Scorched forest[c]		—		0.07	0.63
Clearcut[c]		—		0.05	0.15

Models are linear unless noted otherwise. Footnotes indicate tests of alternative models with poorer fit. Significance ($P \le 0.05$) is indicated by bold font

[a] Cover was square-root transformed

[b] Linear model also tested

[c] Peaking model also tested

richness of forest species also tended to decline with time as richness of early-seral and non-forest species increased (Fig. 5).

In contrast to richness, we did not hypothesize that heterogeneity would increase because we expected evenness to decline. Trends in heterogeneity were largely consistent with this expectation, increasing only in BD (Table 2, Fig. 1d). Except for a significant decline in BDS (Table 2), however, evenness changed minimally (Fig. 1d). Heterogeneity and evenness did not differ significantly among site types reflecting large variation among sites within types.

Species gain, loss and turnover (*H*4)

We hypothesized that rates of species' gain would exceed rates of loss. Site-type patterns were largely consistent with expectation, except at the last sampling interval in S and CC, when gains and losses were comparable (Fig. 6). As predicted, rates of gain declined significantly with time, but losses did not, resulting in a gradual decline in turnover (Fig. 6). Although we hypothesized lower rates of gain in BDS (where post-eruption survival was greatest), gains did not differ significantly among site types (Fig 6).

Species composition (*H*5)

We predicted that the composition of BD and S would diverge from CC, as forest species replaced early-seral colonists. Instead, individual sites, and site types more generally, followed parallel trajectories (Fig. 7a, b). BDS sites, characterized by surviving forest species (Fig. 7c), were compositionally distinct from other sites (high scores along NMS1; Fig. 7a, b). CC sites tended to have lower scores along NMS1. S sites,

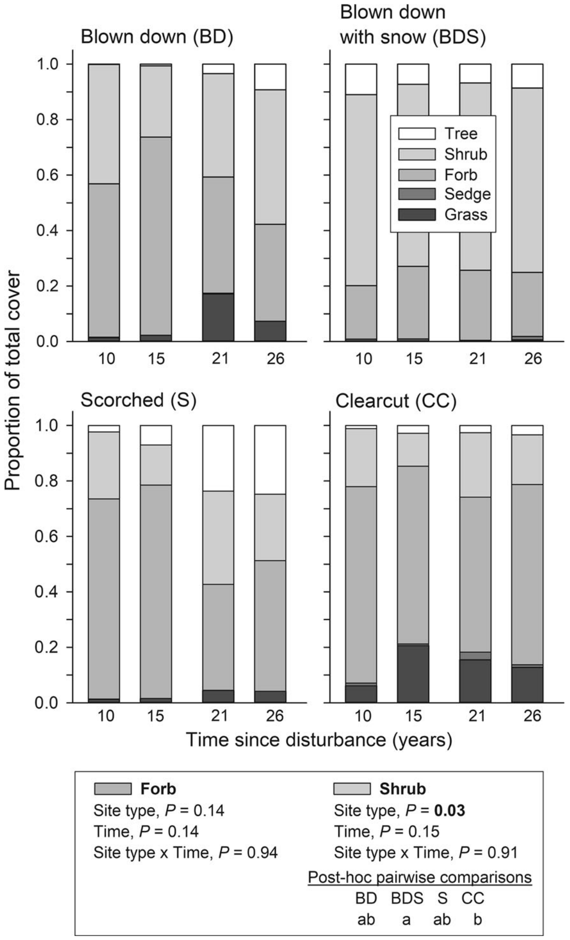


Fig. 2 Temporal trends in relative cover of life forms. In post hoc comparisons, site types with the same letter do not differ significantly. See Fig. 1 for other details

which varied in both species and life form composition, were widely distributed along NMS1 (Fig. 7b). Although turnover in species composition (expressed by trajectory length) varied among sites, the direction of change was fairly consistent: right to left along NMS1 and bottom to top along NMS2 (Fig. 7a, b). These directional changes were correlated with increasing cover of early-seral forbs and grasses, but also a shift in their composition, from dominants of the early post-eruption period (*Epilobium angustifolium* and *Anaphalis margaritacea*) to others with relatively broad (*Hypochaeris radicata)* or more restricted spatial distributions (e.g., *Lotus purshianus* and *L. corniculatus*) (Fig. 7c). NMS3 separated S from other site types; higher scores corresponded to increasing cover of species typical of warmer, less snow-influenced sites.

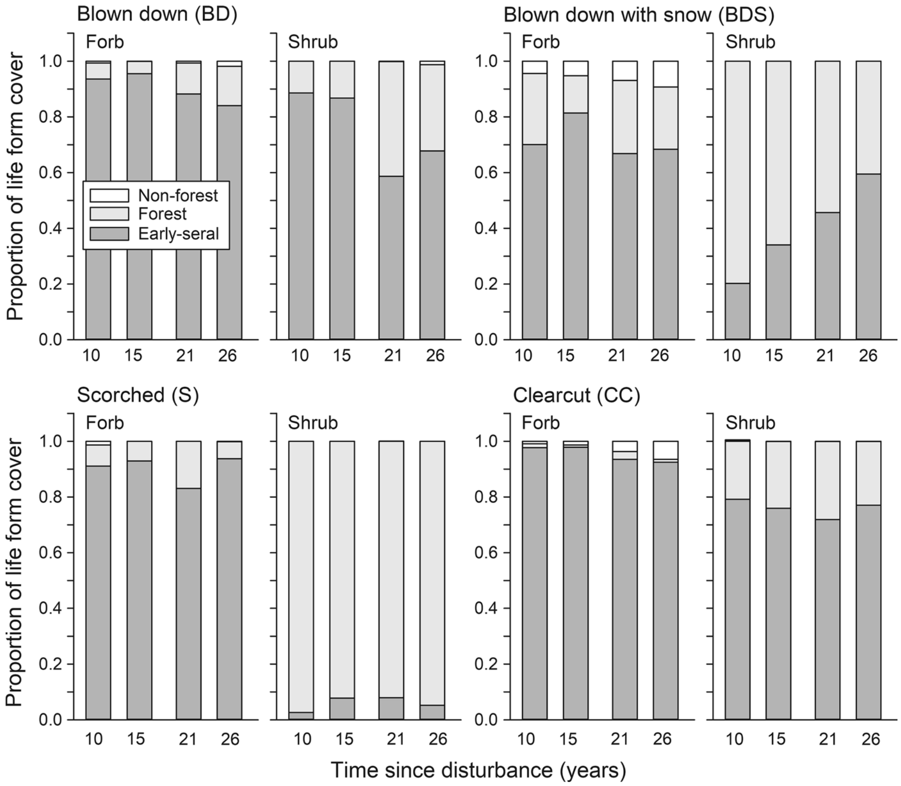
Discussion

The 1980 eruption of Mount St. Helens decimated nearly 500 km^2 of forest north of the volcano. The lateral blast left trees either flattened or standing, stripped of foliage and fine branches, with primary and secondary eruptions depositing as much as 60 cm of tephra. Disturbance theory and early observations of the blast zone suggested that vegetation recovery would be slow, shaped by multiple factors acting prior to, during, and after the eruption. Key among these were disturbance severity, presence of snowpack at the time of the eruption, and pre-disturbance seral state—factors integral to the site-type classification (Halpern et al. 1990). Despite strong contrasts in these factors, we were unable to detect consistent differences among site types for most community attributes. Heterogeneity in ecosystem reassembly is characteristic of large, infrequent disturbances (LIDs; Turner et al. 1998), including volcanic eruptions (Clarkson 1990; Tsuyuzaki 1991; Grishin et al. 1996; del Moral 2000). Although our understanding of heterogeneity in this ecosystem would benefit from a larger sample of the post-eruption landscape (the current sample represents a very small fraction), our long-term measurements provide a rare picture of the recovery process, offering insights into the factors responsible for variation in space and time.

Temporal trends and sources of plant recovery

We expected plant cover to increase and dominance to shift from lower-statured forbs to taller shrubs, consistent with the classical model of succession (Clements 1916). Although cover increased into the third decade in most site types, there was considerable variation in the transition among life forms, both within and among types. For example, in the scorched zone, forbs persisted as dominants in two of three sites, but were replaced by shrubs and trees in the third. Here, the transition to shrub dominance was driven by regrowth of surviving shrubs (*Acer circinatum* and *Gaultheria shallon*), as is common after fire (Haeussler and Coates 1986; Halpern 1989). Early-seral shrubs contributed minimally, in contrast to their

Fig. 3 Temporal trends in relative cover of early-seral, forest, and non-forest forbs and shrubs. See Fig. 1 for other details



dominance after fire (Schoonmaker and McKee 1988; Halpern and Franklin 1990). Their scarcity likely reflected burial of the soil seed bank by tephra and limited dispersal of bird-dispersed fruits into the barren, post-eruption landscape. Those that did establish were mostly wind-dispersed species (*Salix* spp. and *Alnus sinuata*), as is common in primary successional systems (e.g., Tsuyuzaki 1991; Chapin et al. 1994; Grishin et al. 1996). With the exception of a single scorched site at the perimeter of the blast zone, conifer cover was also sparse, suggesting that tree recruitment is seed limited (Turner et al. 1998; del Moral and Magnusson 2014).

In clearcuts, plant cover increased more slowly and without a shrub layer. Forest shrubs were particularly uncommon. Although these may have been herb-dominated communities prior to harvest (Brockway et al. 1983; Topik et al. 1986), the absence of woody survivors may also reflect repeated high-severity disturbance (logging, broadcast burning, physical scouring, and burial by tephra). Although most forest shrubs are tolerant of physical damage or fire, recurrent disturbance with little time for recovery—exacerbated by the harsh, post-eruption environment—may have exceeded thresholds of survival for many shrubs (Romme et al. 1998), resulting in a structurally impoverished vegetation.

In sharp contrast, the strong tempering effect of a spring snowpack remained prominent in blown-down forests with snow. In these topographically shaded sites, shrubs and small trees were protected from the heat of the blast and subsequent snowmelt promoted cracking and slumping of the tephra, facilitating re-emergence (Means et al. 1982; McKee et al. 1987; Halpern et al. 1990). Although forest shrubs dominated for two decades, recent expansion of *Alnus sinuata* in two of the three sites represents a novel transition to dominance by an early-seral shrub. As a nitrogen-fixer adapted to snow-influenced sites, *A. sinuata* can facilitate ecosystem recovery in nutrient-poor soils. However, it can also be a strong competitor for soil resources (Chapin et al. 1994). Its taller stature, sprawling growth form, and competitive ability appear to have slowed what had initially been a more rapid succession to closed-forest species in these snow-protected sites.

In contrast to other site types, blown-down forests showed a consistent downturn in total cover at the last

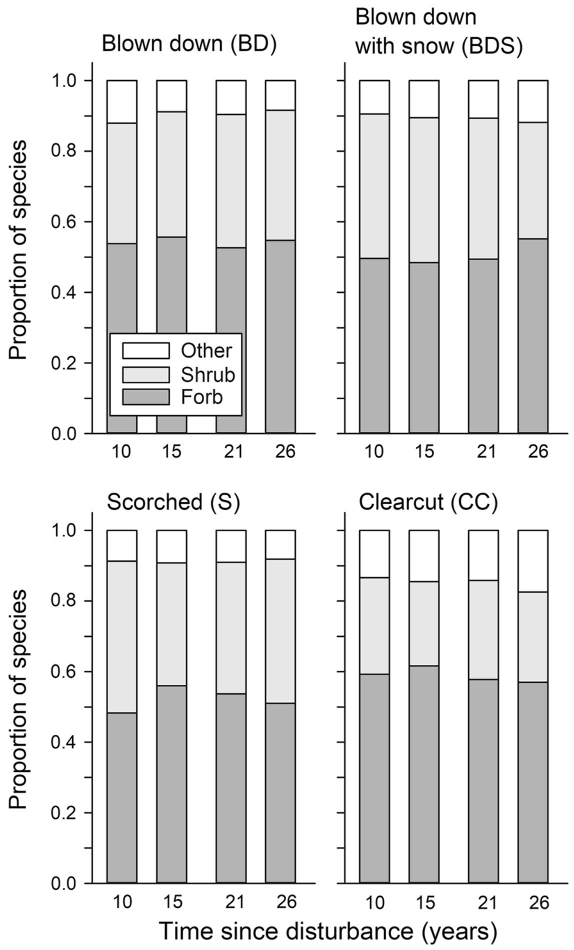


Fig. 4 Temporal trends in proportion of forb, shrub, and other species. 'Other' includes grass, sedge/rush, and tree species. See Fig. 1 for other details

measurement. Within each site, multiple species (mostly early-seral forbs, but some shrubs) declined in parallel, despite the availability of open space. Although competition is assumed to drive species' replacement during succession (Connell and Slatyer 1977; Tilman 1985), other factors may also contribute, including plant longevity, nutrient limitations, allelopathy, predation, or other stressors (Adachi et al. 1996; Halpern et al. 1997; Bishop 2002). In this study, the synchronous decline of early-seral species in blown-down forest, but not in other site types, remains a puzzle.

Compared to other LIDs, vegetation recovery in the blast zone is proceeding slowly. For example, in similar forests, understory cover can exceed 100% within 3–5 years after logging and burning (Schoonmaker and McKee 1988; Halpern and Franklin 1990). The spatial scale and severity of the blast do not fully explain the slower pace of revegetation, as recovery can be fairly rapid after large and severe fires (Turner et al. 1997). Rather, it appears related to the persistent effects of tephra, which can suppress germination from the soil seed bank and vegetative re-emergence of buried plants. Annuals forbs and early-seral shrubs, which can dominate the seed bank (Kellman 1970, 1974; Conard et al. 1985; Harmon and Franklin 1995; Halpern et al. 1999), remained buried by tephra. As a consequence, annuals were a minor component of the vegetation (with the exception of one clearcut site that supported an expanding population of *Lotus purshianus*; Online Resources 2). Similar suppression of the annual seed bank by tephra has been observed in other volcanic systems

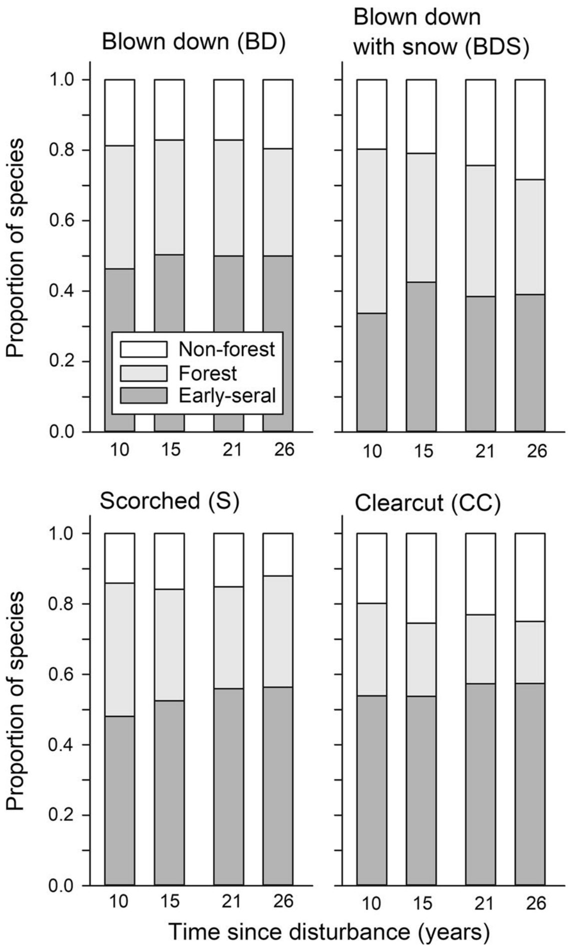
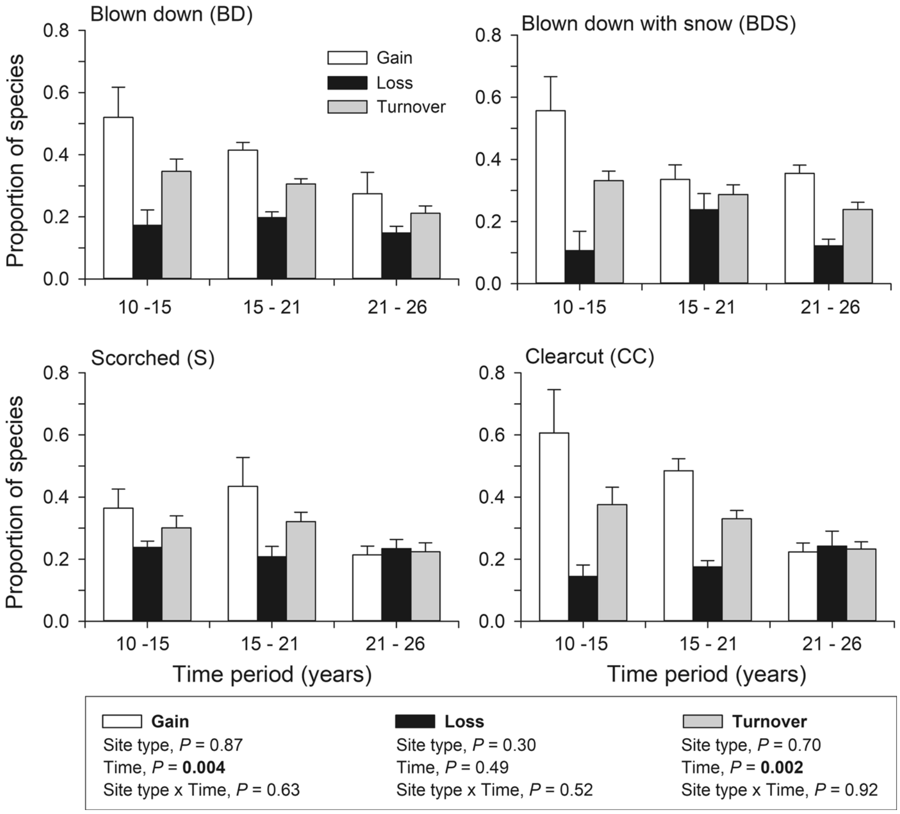


Fig. 5 Temporal trends in proportion of early-seral, forest, and non-forest species. See Fig. 1 for other details

Fig. 6 Temporal trends in species' gain, loss, and turnover. See Fig. 1 for other details

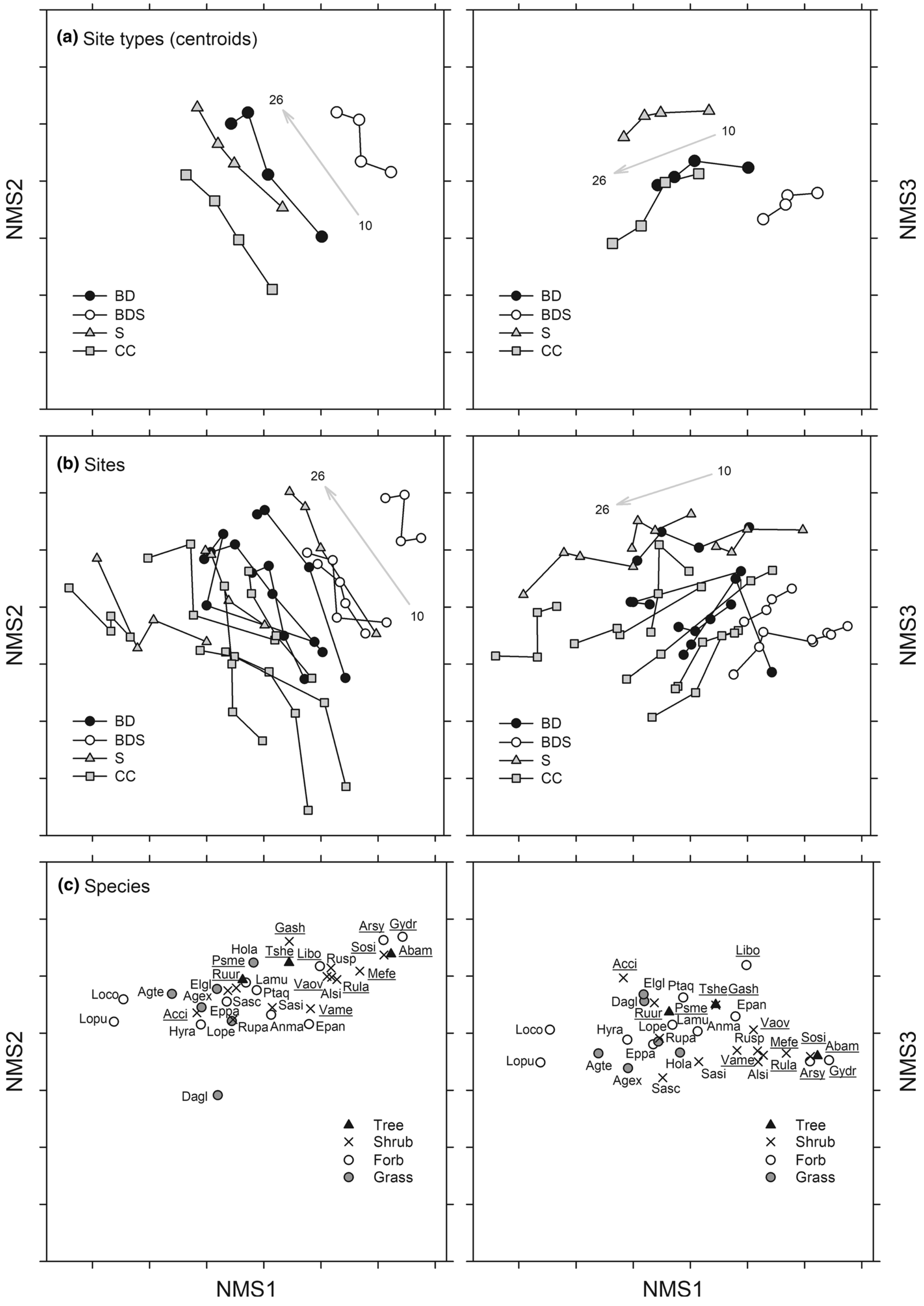


(Tsuyuzaki 1991, 1995). Burial by tephra also constrained vegetative recovery of forest herbs. Although most herbs can resprout from roots, rhizomes, or other regenerative structures after physical damage or fire (Haeussler and Coates 1986, Halpern 1989), deep and persistent burial by tephra can impose a strong filter (Griggs 1918, 1919; Smathers and Mueller-Dombois 1974; Antos and Zobel 1984; Tsuyuzaki 1995). To survive, species must establish new root systems or move perennating structures into the tephra (before carbohydrate reserves are exhausted), or they must emerge annually from root systems in the original soil (an energetically costly strategy if tephra is deep; Antos and Zobel 1985a, b, 1987). Although forest herbs were among the first plants to re-appear in the blast zone, their ongoing colonization of plots and low overall abundance suggest that most individuals were lost to physical disturbance or burial, and that survivors are physiologically stressed by current growing conditions (full sun and droughty, nutrient-poor soils; Chapin and Bliss 1989; Tsuyuzaki 1991; Grishin et al. 1996).

Fig. 7 NMS ordination of compositional changes through time ▶ showing **a** site types (centroids of 3–6 sites) **b** sites, and **c** common species (> 1% cover in a site type). Left and right columns are different pairs of axes. Grey arrows indicate the general direction of change from year 10 to 26. Forest species are underlined; early-seral species are not. Species are: Abam (*Abies amabilis*), Acci (*Acer circinatum*), Agex (*Agrostis exarata*), Alsi (*Alnus sinuata*), Anma (*Anaphalis margaritacea*), Arsy (*Aruncus sylvester*), Dagl (*Dactylis glomerata*), Elgl (*Elymus glaucus*), Epan (*Epilobium angustifolium*), Eppa (*E. paniculatum*), Gydr (*Gymnocarpium dryopteris*), Gash (*Gaultheria shallon*), Hola (*Holcus lanatus*), Hyra (*Hypochaeris radicata*), Libo (*Linnaea borealis*), Loco (*Lotus corniculatus*), Lamu (*Lactuca muralis*), Lope (*Lolium perenne*), Lopu (*Lotus purshianus*), Mefe (*Menziesia ferruginea*), Psme (*Pseudotsuga menziesii*), Ptaq (*Pteridium aquilinum*), Rula (*Rubus lasiococcus*), Rupa (*R. parviflorus*), Rusp (*R. spectabilis*), Ruur (*R. ursinus*), Sasc (*Salix scouleriana*), Sasi (*S. sitchensis*), Sosi (*Sorbus sitchensis*), Tshe (*Tsuga heterophylla*), Vame (*Vaccinium membranaceum*), Vaov (*V. ovalifolium*)

Rates and sources of species colonization and loss

As predicted, species continue to accumulate in the blast zone after more than two decades. In fact, over the 16-year study period, gamma diversity increased


(a) Site types (centroids)
26
10
BD
BDS
S
CC
(b) Sites
(c) Species
Gash
Arsy
Gydr
Hola
Tshe
Libo
Sosi
Abam
Psme
Rusp
Mefe
Ruur
Lamu
Vaov
Rula
Elgl
Loco
Agte
Agex
Ptaq
Alsi
Sasc
Sasi
Vame
Lopu
Acci
Eppa
Hyra
Lope
Rupa
Anma
Epan
Dagl
Tree
Shrub
Forb
Grass
NMS2
NMS3
NMS1

nearly 40% (from 124 to 173 species) and local (site-scale) diversity nearly 50%. On the other hand, we anticipated greater colonization of clearcut (species-poor) than snow-influenced (richer) sites, but rates of gain have remained surprisingly similar, driven by the ubiquitous and continuing recruitment of early-seral forbs. At the same time, rates of loss have been low and unrelated to time. These patterns of gain and loss suggest that safe sites remain available for colonization of early-seral forbs, and biotic controls on establishment and persistence are weak (Tilman 2004; Anderson 2007). On the other hand, species' heterogeneity and evenness have not kept pace with richness, suggesting that most recent immigrants have contributed minimally to cover, with early-seral dominants in most sites having established in the first decade.

As anticipated, rates of colonization gradually declined with time, a natural consequence of a fixed species' pool, dispersal limitation, and abiotic/biotic constraints on establishment (Myster and Pickett 1994; Anderson 2007). Distances to seed sources in or adjacent to the blast zone pose barriers to establishment (Turner et al. 1998; del Moral and Magnusson 2014). Newly recruiting species were largely early-seral, reflecting the prevalence of long-distance dispersal mechanisms in this group. In contrast, most forest herbs disperse over short distances (Bierzychudek 1982; Cain and Damman 1997; Matlack 2005) and seed production can be infrequent (Whigham 2004; Lindh 2005; Zobel and Antos 2007, 2016). Moreover, for seeds that are dispersed, physical exposure and coarse, infertile soils may limit germination and early survival of forest species. However, as trees establish, overstory canopies close, and litter accumulates, we expect significant and predictable shifts in the relative contributions of early-seral and forest species to patterns of loss and gain.

Compositional changes

Local patterns of succession within LIDs can be diverse and unpredictable, reflecting the complex and temporally varying effects of disturbance, survival, abiotic variation, dispersal, biotic interactions, and chance (Christensen and Peet 1984; Halpern 1988; del Moral et al. 1995; Turner et al. 1998). Successional trajectories can diverge if disturbance or environmental variation act as filters on survival or recruitment (Halpern 1988; Lepš and Rejmánek 1991; Matthews and Spyreas 2010; Zobel and Antos 2017), or if chance establishment leads to priority effects (Fukami et al. 2005; del Moral 2007; del Moral et al. 2010). Conversely, trajectories can converge if abiotic conditions become more similar, if the same group of colonists invades to dominate multiple sites, or if more diverse communities of ruderals are replaced by fewer competitive species (Connell and Slatyer 1977; Christensen and Peet 1984). Counter to expectation, we saw little evidence of divergence among sites or site types. Despite significant turnover in composition (35–60% of species), sites progressed in parallel, retaining strong legacies of pre-eruption seral state (clearcuts poor in forest shrubs), pre-eruption composition (related to location or elevation), or disturbance severity (shrub loss reduced by snow cover or distance from the blast). Nevertheless, early-seral forbs remained the most abundant and dynamic group, with dominants of the early post-eruption period (*Epilobium angustifolium* and *Anaphalis margaritacea*) gradually replaced by a diversity of perennial colonists, including species with relatively broad, as well as more restricted distributions.

Conclusions

The cataclysmic eruption of Mt. St. Helens created a large and heterogeneous post-disturbance landscape. Plant recovery is proceeding slowly and variably through both primary and secondary successional processes. Despite severe heating and physical scouring by the blast, tephra deposits may be a more persistent control on recovery, both as a barrier to plant re-emergence and as the primary substrate for colonization. Twenty-six years after the eruption, plant cover averages ~ 50% and species continue to accumulate, albeit at a decelerating pace. The pioneering forb community has remained a dominant, but dynamic, component of the vegetation, except where a protective snowpack tempered the effects of the blast. Closed-forest herbs remain under-represented, a consequence of poor survival, seed limitation, and abiotic constraints on establishment. In sum, the seral composition and structure of these communities remain distinctly different from those of the mature and older forests that characterized the pre-eruption landscape. Major changes in vegetation structure or seral composition are not likely to occur until conifers recolonize and alter light and edaphic conditions. Their slow and localized recruitment suggest that isolation from seed sources may be the principal constraint on forest development. However, as initial colonists mature and produce seed, the pace of forest recovery will accelerate.

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