




# Testing conceptual models of early plant succession across a disturbance gradient

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## Abstract

1. Studies of succession have a long history in ecology, but rigorous tests of general, unifying principles are rare. One barrier to these tests of theory is the paucity of longitudinal studies that span the broad gradients of disturbance severity that characterize large, infrequent disturbances. The cataclysmic eruption of Mount St. Helens (Washington, USA) in 1980 produced a heterogeneous landscape of disturbance conditions, including primary to secondary successional habitats, affording a unique opportunity to explore how rates and patterns of community change relate to disturbance severity, post-eruption site conditions and time.
2. In this novel synthesis, we combined data from three long-term (c. 30-year) studies to compare rates and patterns of community change across three 'zones' representing a gradient of disturbance severity: primary successional blast zone, secondary successional tree blowdown/standing snag zone and secondary successional intact forest canopy/tephra deposit zone.
3. Consistent with theory, rates of change in most community metrics (species composition, species richness, species gain/loss and rank abundance) decreased with time across the disturbance gradient. Surprisingly, rates of change were often greatest at intermediate-severity disturbance and similarly low at high- and low-severity disturbance. There was little evidence of compositional convergence among or within zones, counter to theory. Within zones, rates of change did not differ among 'site types' defined by pre- or post-eruption site characteristics (disturbance history, legacy effects or substrate characteristics).
4. *Synthesis.* The hump-shaped relationships with disturbance severity runs counter to the theory predicting that community change will be slower during primary than during secondary succession. The similarly low rates of change after high- and low-severity disturbance reflect differing sets of controls: seed limitation and

abiotic stress in the blast zone vs. vegetative re-emergence and low light in the tephra zone. Sites subjected to intermediate-severity disturbance were the most dynamic, supporting species with a greater diversity of regenerative traits and seral roles (ruderal, forest and non-forest). Succession in this post-eruption landscape reflects the complex, multifaceted nature of volcanic disturbance (including physical force, heating and burial) and the variety of ways in which biological systems can respond to these disturbance effects. Our results underscore the value of comparative studies of long-term, ecological processes for testing the assumptions and predictions of successional theory.

#### KEYWORDS

community assembly, disturbance severity, legacy effect, Mount St. Helens, primary succession, secondary succession, temporal change, volcano ecology

## 1 | INTRODUCTION

The long history of research on ecological succession has provided insights into how communities respond to disturbance (e.g. Cowles, 1899; Clements, 1916; Eglar, 1954; Connell & Slatyer, 1977; Chapin, Walker, Fastie, & Sharman, 1994; Walker & del Moral, 2003; Prach & Walker, 2011; Meiners, Cadotte, Fridley, Pickett, & Walker, 2014; Walker & Wardle, 2014; Egerton, 2015). The compositional changes that characterize succession are the product of multiple factors, including disturbance characteristics, site history, dispersal limitation, abiotic stressors and biotic interactions that operate at a range of spatial scales (Franklin, 1990; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Måren, Kapfer, Aarrestad, Grytnes, & Vandvik, 2018; del Moral & Titus, 2018; Norden et al., 2015; Pickett, Collins, & Armesto, 1987; Prach & Walker, 2011; Walker & del Moral, 2003). The relative importance of these factors should vary across gradients in disturbance severity. For example, the roles of site history and biological legacies should decline with disturbance severity as abiotic stressors and dispersal limitation become increasingly important.

Theory suggests that rates and patterns of community change will vary predictably across gradients of disturbance severity (Turner, Baker, Peterson, & Peet, 1998; Walker & del Moral, 2003), although explicit comparisons of these relationships are rare (but see Prach et al., 2016). Volcanic eruptions, characterized by steep gradients in disturbance severity and in the depth and physical properties of air-fall deposits (e.g. ash and pumice), are model systems for testing these predictions (e.g. Grishin, Moral, Krestov, & Verkhohat, 1996). Using a novel synthesis of long-term, longitudinal data, we compare rates and patterns of community change across the primary to secondary successional gradient produced by the cataclysmic eruption of Mount St. Helens, Washington in 1980.

We test three generalizations of successional theory that relate plant community change to disturbance severity and time. They address two fundamental properties of community change: rates and

patterns of change *within* sites (representing points along the severity gradient), and the degree to which sites *converge or diverge* with time (Avolio et al., 2015; Houseman, Mittelbach, Reynolds, & Gross, 2008; Matthews & Spyreas, 2010). The first generalization is that rates of change will be slower during primary than during secondary succession – initiated by higher vs. lower severity disturbance – due to greater propagule limitation, abiotic stress and resource limitation (Glenn-Lewin, Peet, & Veblen, 1992; Miles & Walton, 1993; but see Prach et al., 2016). However, rates of community change will decline over time in both types of seres (Anderson, 2007; Odum, 1969; Walker, 2011; Walker & del Moral, 2003). Second, community convergence is less likely during primary than during secondary succession, reflecting the greater contribution of stochastic (vs. deterministic) processes when site conditions are harsher (Chase, 2007; Kreyling, Jentsch, & Beierkuhnlein, 2011; Måren et al., 2018; but see Prach et al., 2016). Third, rates of community change are most variable (or unpredictable) with intermediate-severity disturbance, where the complex interplay of site history, legacy effects and biotic interactions can produce multiple outcomes (Foster, Knight, & Franklin, 1998; Franklin, 1990; Tilman, 1985).

Long-term studies have made fundamental contributions to our understanding of community succession (Buma, Bisbing, Krapek, & Wright, 2017; Halpern & Lutz, 2013; Harmon & Pabst, 2015; Li, 2016; Walker & del Moral, 2009), yielding insights into patterns and processes that are not easily discerned with the chronosequence approach (Johnson & Miyanishi, 2008; Pickett & McDonnell, 1989; Walker, Wardle, Bardgett, & Clarkson, 2010). Yet, even with longitudinal studies, it can be difficult to identify the underlying mechanisms of compositional change (Anderson, 2007; del Moral & Chang, 2015; Prach & Walker, 2011; Walker & Wardle, 2014). The ability to infer process from pattern can be strengthened, however, by combining multiple lines of evidence. To that end, we explore the behaviour of community metrics that capture different components of compositional change: change in richness, species' turnover (via gain and loss) and change in rank abundance or rank

abundance distribution (incorporating species' gain, loss and relative abundance). In combination, these metrics offer insights into the processes that drive compositional change. For example, species richness may change little (suggesting a slow rate of succession), despite a large, simultaneous loss and gain of species (indicative of turnover). Similarly, shifts in rank abundance may be driven by species turnover (loss and/or gain) or by changes in dominance (via differing rates of growth) without turnover. Moreover, the consistency with which species contributes to turnover or changes in rank offer insights into the importance of stochastic vs. deterministic processes. For example, consistent shifts in rank abundance among species would be indicative of deterministic processes, supportive of the Clements' (1916) model of succession. In contrast, variation in the identity or timing of species' dominance would be indicative of stochastic processes (e.g. priority effects) or other historical contingencies (e.g. past disturbance or legacy effects; Foster et al., 1998; Turner et al., 1998; Fukami, Martijn Bezemer, Mortimer, & Putten, 2005; Swanson et al., 2011; Fukami, 2015). Long-term studies of successional change offer an opportunity to explore the relative importance of these processes and how they are shaped by characteristics of the initiating disturbance, variation in the post-disturbance environment and time.

In this study, we combine data from long-term studies conducted independently in areas of differing disturbance severity at Mount St. Helens. Together, they represent a large gradient from (1) high-severity (primary successional 'blast zone') sites devoid of vegetation with new volcanic substrates; through (2) intermediate-severity (secondary successional 'blowdown zone') sites characterized by loss of overstorey trees, major loss of understorey plants and burial by air-fall deposits; to (3) low-severity (secondary successional 'tephra zone') sites with intact forest canopies and understories buried by air-fall deposits. Sites within each of these zones represent different post-eruption habitats (or 'site types') varying in their disturbance or substrate characteristics, site histories and biological legacies. Drawing from theory and previous studies of this system, we hypothesized the following patterns of community change across the disturbance gradient:

H1: Rates of community change would be lowest in the high-severity, primary successional blast zone, where propagule limitation and abiotic stress are greatest. However, with time, rates of change would decline in all zones.

H2: Compositional convergence would be lowest among sites in the primary successional blast zone, where harsher site conditions increase the likelihood of stochastic processes. However, with time, deterministic processes would promote convergence within and among zones.

H3: Rates of community change would differ among 'site types' within each zone, but would be greatest at

intermediate-severity disturbance, where site types encompass the greatest variation in site history and legacy effects.

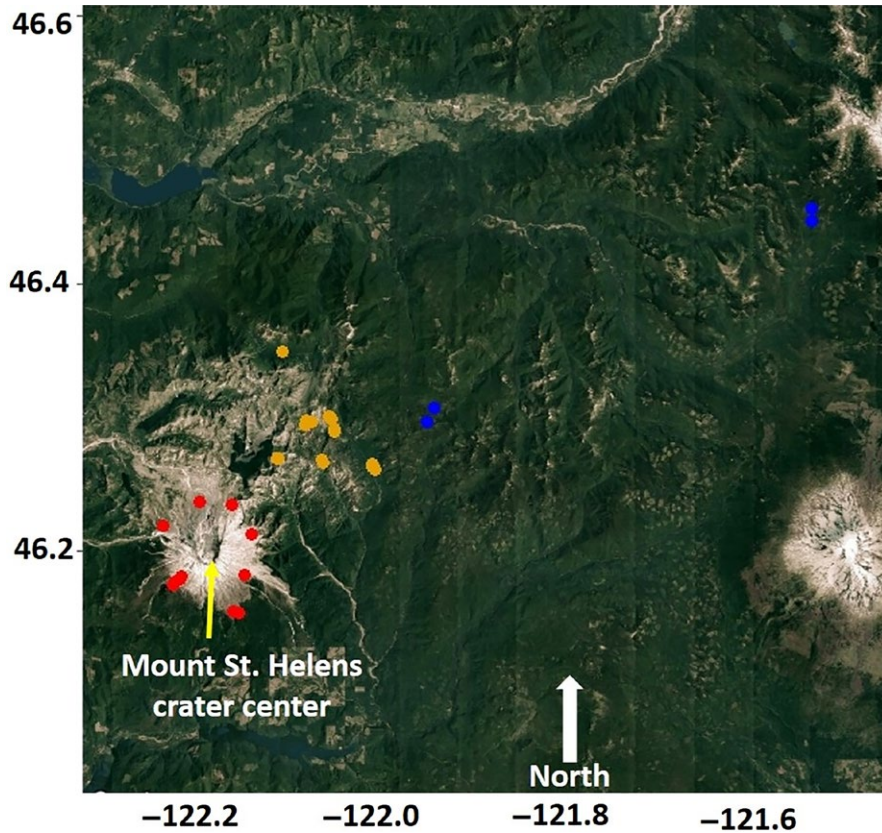
## 2 | MATERIALS AND METHODS

### 2.1 | Study systems and the disturbance-severity gradient

Our studies occurred on or near Mount St. Helens, Washington, USA (46.1912°N, 122.1944°W), among sites that spanned the disturbance gradient created by the 1980 eruption. Mount St. Helens (pre- and post-eruption elevations of 2,950 and 2,549 m) is a Quaternary stratovolcano in the Cascade Range of southern Washington, composed largely of dacite and andesite. It has erupted frequently over the last 4,000 years (Mullineaux, 1986; Sarna-Wojcicki, Shipley, Waitt, Dzurisin, & Wood, 1981), depositing tephra (aerial ejecta of ash or pumice) to varying depths, although the lateral nature of the 1980 blast may be an unusual feature of its eruption history (Lipman & Mullineaux, 1981). The pre-eruption vegetation included mature and old-growth forests characteristic of the western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*) vegetation zones, with some higher elevation sites extending into the mountain hemlock (*Tsuga mertensiana*) zone and non-forested portions of the sub-alpine zone (Franklin & Dyrness, 1973).

The eruption created a large (>500 km<sup>2</sup>), heterogeneous landscape of habitats encapsulated by three 'disturbance zones' of decreasing severity: blast, blowdown and intact forest/tephra (Figure 1, Table 1). Disturbance severity decreased with distance from the crater to the north but changed little to the south due to the lateral orientation of the blast (Dale, Swanson, & Crisafulli, 2005). Each of these zones is characterized by a range of post-eruption habitats (or 'site types') reflecting variation in elevation and topography, mechanisms of disturbance (e.g. blast, scour or lahar), texture or depth of deposit, snowpack at the time of the eruption and disturbance history (Table 1). We briefly review the distinguishing features and sources of variation within each zone. The *blast zone* is a primary successional area where severe disturbance (intense lateral blast, heat and scour) and subsequent deposits of pumice or tephra destroyed, removed or buried existing vegetation and soil (Dale et al., 2005), leaving only isolated refugia (del Moral, Wood, & Titus, 2005). Succession proceeded on bare rock, colluvium or pumice. We included five site types in this study: blast only (sampled with two sites), blast and pumice deposit (two sites), blast and tephra deposit (five sites), scour (two sites) and lahar/mudflow (one site) (12 sites in total; Table 1).

The *blowdown zone*, representing intermediate-severity disturbance, is a secondary successional area where the strong lateral force and heat of the eruption toppled or otherwise killed mature or old-growth trees. Some, but not all, of the understorey vegetation was killed by the heat of the blast and original soil was buried under 10–60 cm of tephra. In some higher elevation, topographically sheltered sites, late-lying snow protected the understorey from the heat



**FIGURE 1** Map of the Mount St. Helens landscape showing the locations of sample sites among the three zones representing the disturbance-severity gradient: blast (red), blowdown (orange) and tephra (blue)

**TABLE 1** Disturbance zone characteristics (distance from crater and elevation), numbers of sites per site type, sampling designs and sampling years. For consistency, comparisons among disturbance zones were based on years during which all zones were sampled (1980, 1989, 2000 and 2010)

Disturbance zone	Distance from crater (km)	Elevation (m)	Site type (number of sites)	Site-scale sampling design	Sampling years
Blast	<5–10	1,248–1,550	Blast only (2) Blast + pumice (2) Blast + tephra (5) Scour (2) Lahar (1)	24, 0.25-m <sup>2</sup> quadrats in each of 3–12, 250-m <sup>2</sup> circular plots; plots spaced 50–100 m apart along one or more transects	Annually 1980–2010, 2015
Blowdown	11–17	710–1,250	Blowdown (3) Blowdown + snow (3) Scorch (3) Clearcut (5)	3, 250-m <sup>2</sup> circular plots spaced 50 m apart along a transect	Annually 1980–1984, 1986, 1989, 1994, 2000, 2005, 2010, 2015 or 2016
Tephra	22, 58	1,160–1,290	Deep tephra (2) Shallow tephra (2)	100, 1-m <sup>2</sup> quadrats spaced 2 m apart along multiple transects	Annually 1980–1983, 1989 or 1990, 2000, 2005, 2010, 2016

of the blast, resulting in markedly greater survival, particularly of woody species (Cook & Halpern, 2018; Halpern, Frenzen, Means, & Franklin, 1990). At the margins of this zone, where blast forces were reduced, trees were scorched and killed but remained standing. This zone also included ‘clearcut’ sites that had been logged, burned and replanted 1–12 years prior to the eruption. Four site types were defined encompassing these multiple sources of variation: blown-down forest (sampled at three sites), blown-down forest with snow

(three sites), scorched forest (three sites) and clearcut (five sites) (14 sites in total; Table 1).

The *tephra* zone represents the low-severity end of the disturbance gradient. The old-growth canopy remained largely intact, but the understorey was buried by tephra of varying texture (coarse lapilli to fine ash) and depth (Zobel & Antos, 1991, 1997, 2017). In contrast to the blowdown zone, snowpack at the time of the eruption reduced survival of woody plants because stems flattened by snow remained

trapped by the tephra following snowmelt (Antos & Zobel, 1982; Zobel & Antos, 1997, 2017). For this study, we included two site types defined by depth of burial: deep (c. 12–15 cm) and shallow (c. 4.5 cm), each sampled with two sites (four in total; Table 1).

Disturbance zones differ in their elevational ranges (Table 1), but share the same regional climate of cool wet winters, warm dry summers and potential for a late-lying snow (Franklin & Dyrness, 1973). Sites in the blast zone had the highest elevational range (1,250–1,550 m), sites in the blowdown had the lowest range (710–1,250 m) and sites in the tephra zone were intermediate (1,160–1,290 m). Consequently, there was little correlation between disturbance severity and climatic variation due to elevation. In fact, microclimate variation may be as dependent on topography (slope and aspect) or canopy cover (tephra zone only) as on elevation. At a coarse spatial scale, disturbance zones differed in their proximity to post-eruption seed sources: these sources were closer in the secondary successional blowdown and tephra zones than in the primary successional blast zone (Figure 1).

## 2.2 | Sampling methods and data reduction

We use permanent-plot data spanning more than three decades from studies conducted independently in each of these zones. The sampling design and frequency of sampling differed among studies (Table 1). In the blast zone, estimated species' cover was the mean percent cover in 24 quadrats (each 0.25 m<sup>2</sup>) within each 250-m<sup>2</sup> circular plot, with 3–12 plots per site (del Moral, 2010). Trace cover (0.1%) was assigned to species absent from the quadrats but present in the larger plot (del Moral, 2010). In the blowdown zone, cover was visually estimated in units of square centimetres or metres (then converted to %) in each of three, 250-m<sup>2</sup> circular plots per site (Cook & Halpern, 2018; Halpern et al., 1990). In the tephra zone, cover (%) was estimated in 100, 1-m<sup>2</sup> quadrats spaced 2 m apart along multiple transects per site (Zobel & Antos, 1997). Sampling details can be found in del Moral (2010) for the blast zone, Halpern et al. (1990) and Cook and Halpern (2018) for the blowdown zone and Zobel and Antos (1997) for the tephra zone.

To facilitate comparisons among zones, mean cover of each species was generated from quadrat- or plot-scale values at each site. Sites were treated as replicates to ensure that different sampling methodologies among zones did not bias comparisons. Because zones were sampled at different frequencies, analyses were limited to data from years in which all zones were sampled synchronously; these corresponded to ca. 10-year intervals (1980, 1989, 2000 and 2010). However, to assess overlap in species composition among zones, we used the full set of temporal samples.

## 2.3 | Analytical methods

### 2.3.1 | Metrics of community change

To address hypotheses related to rates of community change among (H1 and H2) and within zones (H3), we computed an array of community-change metrics for each site. Values were computed for each

sampling interval ( $t_1$  to  $t_2$ ) except for 'community stability' which encompassed the full study period.

1. 'Community stability' (sensu Tilman, 1999), an index of temporal variation in plant cover, was computed as the mean total (summed) cover of species divided by the standard deviation (SD) of total cover for the four sampling dates. Values were generated with the `community_stability()` function in the `CODYN` R package of R (Hallett et al., 2016).
2. 'Change in composition' was computed as the Euclidean distance between the centroids of successive sampling periods from a principle coordinate analysis based on a Bray–Curtis dissimilarity matrix (Avolio et al., 2015; Avolio et al., in review). Values were computed using the `multivariate_change()` function in the `CODYN` R package (Hallett et al., 2018).
3. 'Change in dispersion' was computed as the difference in mean distance (as above) of individual sites to the zone centroid between successive samples. A positive dispersion value indicates divergence (sites become more dissimilar) and a negative value indicates convergence (sites become more similar).

Five additional change metrics were computed and relativized by the size of the local species pool spanning each interval ( $S_{tot}$ ). This relativization, which accounts for differences in the number or size of sampling units, facilitates comparisons among zones. These metrics were computed using the `RAC_change()` function in the `CODYN` R package (Hallett et al., 2018; Avolio et al., in review):

4. 'Change in richness' was computed as the difference in richness between successive samples ( $t_2 - t_1$ ) divided by  $S_{tot}$ . Positive values indicate an increase and negative values, a decrease.
5. 'Species gain' and 'species loss' were computed as the number of species unique to  $t_2$  or to  $t_1$ , respectively, divided by  $S_{tot}$ .
6. 'Change in rank abundance' was computed as the average of the absolute value of the change in rank of each species from  $t_1$  to  $t_2$ , divided by  $S_{tot}$ . Species absent at  $t_1$  or  $t_2$  were assigned a shared rank of  $n + 1$ , where  $n$  is the number of species present at  $t_1$  or  $t_2$ .
7. Change in rank abundance curve shape was computed as the difference in area between cumulative abundance curves representing  $t_1$  and  $t_2$ , as described by Hallett et al. (2018) and Avolio et al. (in review). To aid in the interpretation of rank abundance metrics, we identified the species contributing most to changes in rank using the `abundance_change()` function in the `CODYN` R package (Hallett et al., 2018; Avolio et al., in review).

Simulations using relativized data suggest that our richness, gain and loss metrics are relatively insensitive to plot size, although rank abundance metrics tend to be lower in samples with five or fewer species (Avolio et al., in review). Species accumulation curves indicate that we captured the vast majority of species in blast- and tephra-zone sites (Carey, Harte, & Moral, 2006,

Fischer et al. unpublished data), but may have missed rarer taxa at later sampling dates in some of the more diverse, high-cover sites in the blow down zone. However, due to their rarity (i.e. infrequency among sites), any such omissions should have minimal effect on zonal comparisons.

### 2.3.2 | Statistical models

We used repeated-measures mixed-effects models (or simpler models as appropriate) to examine the response of each community metric to disturbance severity (disturbance zone) and time (10-year sampling interval) (H1 and H2). We treated zone, time (sampling interval) and their interaction as categorical fixed effects, and site as a random effect (to account for the repeated sampling of sites). Significant main effects or interactions were followed by Tukey HSD tests. Community stability was tested with a simple linear model because time is implicit in the metric. Change in community dispersion was not tested statistically because it represents a zonal, rather than site-scale, attribute. All models were developed using the `lme()` function in the `nlme` R package version 3.1-137 (Pinheiro, Bates, DebRoy, & Sarkar, 2013); *p* values were derived from Wald's *Z* tests.

In addition to these univariate tests, we used ordination (non-metric multidimensional scaling, NMDS) to graphically illustrate patterns of compositional change across the disturbance gradient. NMDS was performed with Bray-Curtis as the distance measure, using `metaMDS()` function in the `vegan` R package version 2.5-3 (Oksanen et al., 2011). The data matrix included the mean cover of each species at each site at each of the four sampling dates. For presentation, site scores along NMDS axes were averaged and plotted as zone centroids ( $\pm 1$  SE) at each point in time. To aid with interpretation, we computed the proportional overlap in species composition among zones.

To test for variation in rates of community change among sites within zones (H3), we employed the same repeated-measures mixed-effects modelling approach, using the same set of community metrics, with the exception of community stability. Separate models were developed for sites within each zone, with site type, time and their interaction treated as fixed effects, and site treated as a random effect.

## 3 | RESULTS

### 3.1 | Variation across the disturbance-severity gradient

We predicted that sites in the blast zone (high-severity disturbance) would show the slowest rates of community change (H1). Rather, we found comparable or lower rates of change in the tephra zone (low-severity disturbance) for most community metrics, including stability, change in composition, change in richness, species gain and change in rank abundance (Figures 2 and 3; Table 2). For these same metrics, rates of change were distinctly greater in the blowdown zone (intermediate-severity disturbance), particularly during the

first sampling interval (significant zone  $\times$  time interactions; Table 2; Figures 2 and 3). Temporal trends were generally consistent with our prediction of a decline in the rate of change over time (H1), with some exceptions. Compositional change (Figure 2c) and change in species rank abundance curve shape (Figure 3d) declined in the blast and tephra zones, but not in the blowdown zone (significant zone  $\times$  time interaction; Table 2). This contrast among zones was also evident in the NMDS ordination: blast- and tephra-zone sites showed little movement in compositional space after the first sampling interval, but blowdown sites showed significant movement during the last interval (Figure 2b).

There was only partial support for our hypotheses about convergence (H2). As predicted, sites in the blast zone showed minimal convergence (change in dispersion close to 0) and sites in the blowdown and tephra zones showed early convergence (change in dispersion  $< 0$ ) (Figure 2d). However, blowdown- and tephra-zone sites subsequently diverged or showed little change in dispersion, counter to expectation. The patterns of movement and separation of zone centroids in NMDS space suggest minimal convergence among zones (Figure 2b), consistent with the small proportion of species found in common ( $< 10\%$ – $20\%$ ; Supporting Information Figure S1).

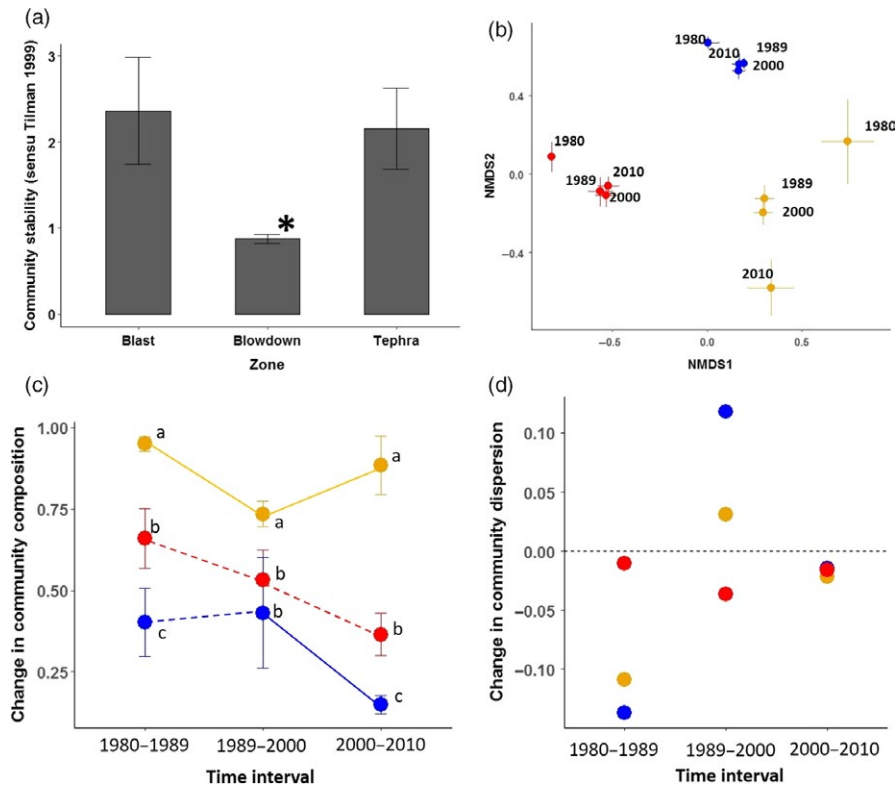
### 3.2 | Variation among site types within disturbance zones

We did not observe significant differences in metrics of community change among site types within zones, counter to expectation (H3) (Table 3). However, we did observe significant declines in rates of change with time for most metrics in most site types (consistent with zonal trends). For several metrics (change in richness, species gain and change in rank abundance), we detected significant site type  $\times$  time interactions. These were limited, however, to the tephra zone (Table 3).

## 4 | DISCUSSION

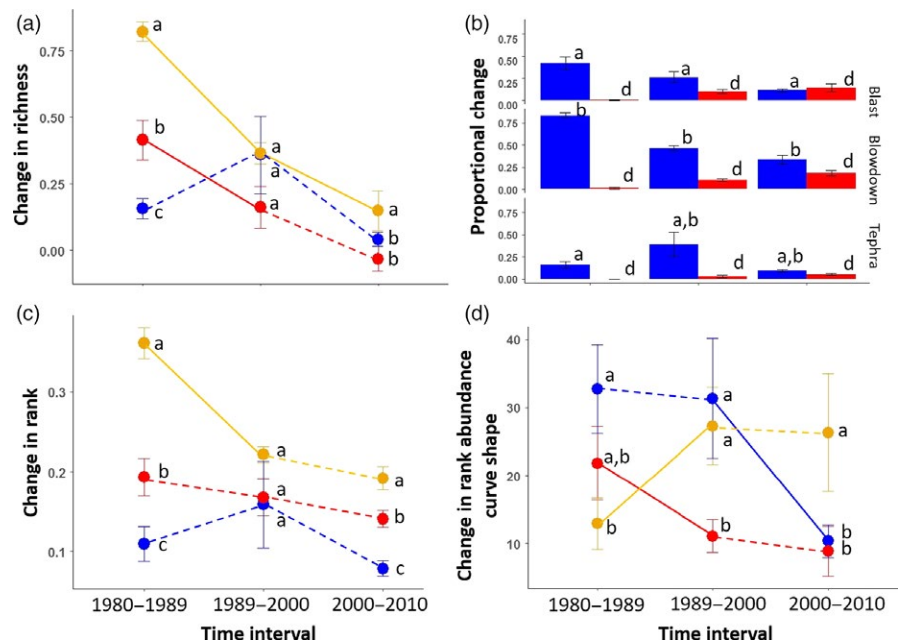
We conducted a novel, comparative analysis of long-term, longitudinal data to test theoretical predictions about rates and patterns of community change along a volcanic-disturbance gradient. The breadth of the disturbance gradient and duration of study allow us to address fundamental aspects of successional theory, including the importance of disturbance severity, post-eruption conditions, legacy effects and time.

Our study challenges the generalization that community change is slower during primary than during secondary succession (Glenn-Lewin et al., 1992; Miles & Walton, 1993). We found comparably slow rates of change at the extremes of the disturbance-severity gradient and more rapid change in the middle. Although there was strong support for the generalization that rates of community change decline during succession (Anderson, 2007; Figures 2 and 3), compositional change did not lead to



**FIGURE 2** Comparisons of (a) community stability (sensu Tilman, 1999) and (b–d) compositional change among and within disturbance zones. For (b–d) zones are coded as red = blast, orange = blowdown and blue = tephra. Values are zone means (or centroids)  $\pm$  1 SE for (a) community stability (1980–2010), (b) NMDS ordination of sites through time and (c) changes in composition (Bray–Curtis dissimilarity) over the three sampling intervals. For (d), change in community dispersion, positive values indicate divergence and negative values indicate convergence of sites within zones. The asterisk in (a) indicates that community stability was lowest in the blowdown zone ( $F = 16.24, p < 0.001$ ). For (c), different lower case letters within a time interval denote significant differences in zone means; solid lines denote significant differences between time intervals within a zone. Repeated-measures mixed-effects model results are presented in Table 2

**FIGURE 3** Comparisons among disturbance zones of five metrics of community change: (a) change in richness, (b) species' gain (blue bars) and loss (red bars), (c) change in rank and (d) change in rank abundance curve shape. For (a), (c) and (d), zones are coded as red = blast, orange = blowdown and blue = tephra. Different lower case letters within a time interval denote significant differences in zone means; solid lines denote significant differences between time intervals within a zone. Repeated-measures mixed-effects model results are presented in Table 2



Community change metric	Predictor	df	den df	F	p
Change in composition	Zone	2	26	28.67	<b>&lt;0.001</b>
	Time	1	31	8.50	<b>0.0013</b>
	Zone × Time	2	31	2.92	<b>0.039</b>
Change in richness	Zone	2	26	18.20	<b>&lt;0.001</b>
	Time	1	31	102.32	<b>&lt;0.0001</b>
	Zone × Time	2	31	5.71	<b>0.002</b>
Species gain	Zone	2	26	36.46	<b>&lt;0.0001</b>
	Time	1	31	71.22	<b>&lt;0.0001</b>
	Zone × Time	2	31	4.93	<b>&lt;0.0001</b>
Species loss	Zone	2	26	2.96	0.082
	Time	1	31	46.64	<b>&lt;0.0001</b>
	Zone × Time	2	31	1.90	0.44
Change in rank abundance	Zone	2	26	31.52	<b>&lt;0.0001</b>
	Time	1	31	38.91	<b>&lt;0.0001</b>
	Zone × Time	2	31	6.38	<b>0.0015</b>
Change in rank abundance curve shape	Zone	2	26	1.38	0.26
	Time	1	31	0.12	0.082
	Zone × Time	2	31	16.30	<b>&lt;0.0001</b>

**TABLE 2** Results of repeated measures mixed-effects models testing for differences in metrics of community change among disturbance zones (Zone) and sampling intervals (Time). Significant effects ( $p \leq 0.05$ ) are indicated in bold. Also see Figures 2 and 3

community convergence either within or among disturbance zones. Succession appears to be proceeding across the disturbance gradient as a nonlinear, spatially idiosyncratic and decelerating process, shaped by different sets of controls that can yield very similar (or very different) outcomes.

#### 4.1 | Variation in succession across the disturbance-severity gradient (H1)

We predicted that community change would be slowest in the high-severity, primary successional blast zone (H1). However, the pattern was more complex – changes were slow in the blast zone (as expected), equally slow in the low-severity tephra zone and higher in the intermediate-severity blowdown zone. Past work in this and other volcanic landscapes suggests that different factors have constrained rates of change in the blast and tephra zones. Two regenerative processes, colonization by seed and vegetative re-emergence, are key, and the factors controlling these processes likely differ at opposite ends of the disturbance gradient. In the blast zone (lacking biological legacies), community development hinges on colonization from seed. Here, as in other primary successional systems, establishment can be seed limited (Makoto & Wilson, 2016; Titus & Bishop, 2014; Wood & del Moral, 2000) or site limited (e.g. high irradiance, strong evaporative demand or infertile soils; Chapin & Bliss, 1989; Tsuyuzaki & del Moral, 1995; Walker, Clarkson, Silvester, Clarkson, & R., 2003; Buma et al., 2017). Even if seedlings are able to establish, these same stressors can limit growth. As a result, colonizers of the blast zone comprised a relatively small group (Supporting Information Figure S2b) of moderate- to long-distance dispersers with adaptations to stress

(e.g. nitrogen fixers and deep-rooted perennial grasses and forbs; Wood & del Moral, 1988; Tsuyuzaki & del Moral, 1995; del Moral, 1999; del Moral & Wood, 2012).

In contrast, slow rates of community change in the tephra zone (rich in biological legacies), related to factors limiting re-emergence from the tephra and, secondarily, to recruitment on the surface. For example, species varied in their abilities to penetrate the tephra (Antos & Zobel, 1985), were slower to emerge in deep- than in shallow-tephra sites and were inhibited where snow was present during the eruption (Fischer, Antos, Biswas, & Zobel, 2018b; Zobel & Antos, 1997). As with most clonal forest herbs (Bierzychudek, 1982; Whigham, 2004), recruitment from seed was uncommon (Antos & Zobel, 1986; Zobel & Antos, 1997), likely limited by relatively low levels of light and low rates of flowering (Zobel & Antos, 2016). Thus, it is not surprising that light-demanding ruderals, which dominated the blowdown zone, failed to colonize these forests.

Sites subjected to intermediate-severity disturbance were more dynamic, supporting species with greater diversity of regenerative traits and seral roles (ruderal, forest and non-forest) (Cook & Halpern, 2018). Ruderal forbs, originating in disturbed sites in and out of the blowdown zone, were the primary drivers of change (Cook & Halpern, 2018). Although they play a transient role after other types of disturbance (Halpern, 1989; Swanson et al., 2011), they dominated the blowdown zone for three decades and may remain dominant until trees establish. More rapid change in this zone may also reflect distinct legacies of disturbance and site history: large fallen trees that locally reduced accumulation of tephra (Halpern et al., 1990) and late-lying snow that enhanced survival in the blowdown (Franklin, 1990; Halpern et al., 1990) but decreased survival in the tephra zone (Antos & Zobel, 1982; Zobel & Antos, 2017).



**TABLE 3** Results of repeated measures mixed-effects models testing for differences in metrics of community change among site types (Type) within zones and sampling intervals (Time). Significant effects ( $p \leq 0.05$ ) are indicated in bold. See Table 1 for a listing of site types within each zone

Community change metric	Disturbance zone	Predictor	df	den df	F	p
Change in composition	Blast	Type	4	6	3.53	0.082
		Time	1	6	33.66	<b>0.001</b>
		Type × Time	4	6	2.36	0.17
	Blowdown	Type	3	10	0.28	0.83
		Time	1	13	1.35	0.27
		Type × Time	3	13	0.27	0.84
	Tephra	Type	1	2	2.05	0.29
		Time	1	4	14.62	<b>0.019</b>
		Type × Time	1	4	6.94	0.058
Change in richness	Blast	Type	4	6	2.01	0.21
		Time	1	6	36.00	<b>0.001</b>
		Type × Time	4	6	1.15	0.41
	Blowdown	Type	3	10	0.69	0.58
		Time	1	13	85.01	<b>&lt;0.0001</b>
		Type × Time	3	13	1.14	0.37
	Tephra	Type	1	2	23.39	<b>0.040</b>
		Time	1	4	20.74	<b>0.010</b>
		Type × Time	1	4	24.83	<b>0.008</b>
Species gain	Blast	Type	4	6	3.74	0.073
		Time	1	6	62.70	<b>0.0002</b>
		Type × Time	4	6	3.91	0.068
	Blowdown	Type	3	10	0.46	0.71
		Time	1	13	74.88	<b>&lt;0.0001</b>
		Type × Time	3	13	0.979	0.43
	Tephra	Type	1	2	17.86	0.052
		Time	1	4	11.78	<b>0.027</b>
		Type × Time	1	4	23.64	<b>0.008</b>
Species loss	Blast	Type	4	6	0.59	0.68
		Time	1	6	6.09	<b>0.049</b>
		Type × Time	4	6	0.49	0.75
	Blowdown	Type	3	10	0.89	0.48
		Time	1	13	72.55	<b>&lt;0.0001</b>
		Type × Time	3	13	1.32	0.31
	Tephra	Type	1	2	5.20	0.15
		Time	1	4	30.42	<b>0.005</b>
		Type × Time	1	4	0.60	0.48
Change in rank abundance	Blast	Type	4	6	0.86	0.54
		Time	1	6	9.59	<b>0.021</b>
		Type × Time	4	6	2.26	0.18
	Blowdown	Type	3	10	0.98	0.44
		Time	1	13	62.71	<b>&lt;0.0001</b>
		Type × Time	3	13	1.82	0.19
	Tephra	Type	1	2	4.10	0.18
		Time	1	4	10.61	<b>0.031</b>
		Type × Time	1	4	15.19	<b>0.018</b>

(Continues)

**TABLE 3** (Continued)

Community change metric	Disturbance zone	Predictor	df	den df	F	p
Change in rank abundance curve shape	Blast	Type	4	6	0.91	0.51
		Time	1	6	6.14	<b>0.048</b>
		Type × Time	4	6	2.37	0.16
	Blowdown	Type	3	10	2.77	0.097
		Time	1	13	20.09	<b>0.001</b>
		Type × Time	3	13	1.67	0.22
	Tephra	Type	1	2	0.59	0.52
		Time	1	4	11.01	<b>0.029</b>
		Type × Time	1	4	1.72	0.26

For most community metrics and in most zones, rates of change were greatest in the first decade – consistent with our prediction (H1), successional theory and observations from other systems (Anderson, 2007). Generally, we observed greater rates of compositional change, larger increases in richness, greater gain than loss of species and larger changes in rank abundance early in succession. Over time, declining rates of compositional change in the blast and tephra zones coincided with smaller increases in richness, minimal species' turnover and smaller changes in rank abundance – all indicative of a slowing of succession. We expect future trends in the tephra zone to be similar, unless resource conditions change dramatically (e.g. due to tree mortality of gap formation). In the blast zone, rates of change are unlikely to increase until taller woody species establish and moderate the microclimatic or edaphic conditions that currently limit recruitment and growth (Gómez-Aparicio et al., 2004; Kroiss & HilleRisLambers, 2014; Li & Wilson, 1998; Titus & Bishop, 2014).

In sum, our comparative analyses reveal surprisingly nonlinear patterns of community change shaped by contrasting sets of controls along the disturbance gradient. In this system, intermediate-severity disturbance promotes greater rates of change among species with a greater diversity of life histories, modes of regeneration and growth rates. Additional manipulative experiments are needed to confirm the relative importance and context dependence of these controls on succession.

#### 4.2 | Compositional convergence within and among disturbance zones (H2)

Sites in the blast zone showed little evidence of convergence, consistent with H2, with theoretical predictions and with past studies of the blast zone (del Moral & Chang, 2015; del Moral & Magnússon, 2014). In contrast, sites in both the blowdown and tephra zones converged early in succession, but then diverged or showed little change in dispersion. In the blowdown zone, early convergence was driven by widespread establishment of a small number of wind-dispersed ruderals (*Chamerion angustifolium* and *Anaphalis margaritacea*) that resprouted in clearcuts, giving rise to an abundance of local seed (Halpern et al., 1990). Subsequent divergence reflected their gradual replacement by ruderals and survivors with more limited

distributions (Cook & Halpern, 2018). In the tephra zone, early convergence reflects recovery of species in deep-tephra sites that were prevalent in shallow-tephra sites, with subsequent divergence driven by variation in tree seedling recruitment and the differential loss of species (Fischer et al., 2018b; Zobel & Antos, 2017).

Given limited convergence within zones, it is not surprising that we failed to detect convergence among zones (Figure 2b). Not only did the dominants differ, but also <10%–20% of species were shared among zones (Figure S1). This lack of overlap among zones reflects the combined effects of elevation (Table 1), disturbance severity and isolation: the blast zone supported mostly subalpine (non-forest) species (del Moral, 2009, 2010); the blowdown, a combination of ruderal and forest species (Cook & Halpern, 2018); and the tephra-zone, largely forest species (Zobel & Antos, 2017). In the short term, succession has followed multiple pathways within and among zones, driven by the interaction of disturbance, biological legacies, local environment and chance (Cook & Halpern, 2018; Fischer, Antos, Grandy, & Zobel, 2016; Halpern et al., 1990; del Moral & Chang, 2015; del Moral & Titus, 2018; Zobel & Antos, 2017). Given the slow pace of tree establishment (Cook & Halpern, 2018; del Moral & Magnússon, 2014), convergence of blast- and blowdown- on tephra-zone forests may take centuries to millennia (Grishin et al., 1996; Prach et al., 2016) and it may occur through multiple pathways (Buma et al., 2017; Donato, Campbell, & Franklin, 2012; Fastie, 1995; Norden et al., 2015).

#### 4.3 | Variation in rates of change among site types within disturbance zones (H3)

We predicted that rates of community change would vary among site types within zones (H3), driven by factors other than disturbance severity (site history, legacy effects, physical environment and substrate characteristics). Moreover, we predicted greater variation at intermediate-severity disturbance, reasoning that high-severity disturbance would erase sources of pre-eruption variation in the blast zone, and effects of tephra depth would be subtle in the low-severity tephra zone. Despite differences in species composition, rates of community change varied little among site types (Table 3), even among those in the blowdown zone, characterized by strong contrasts in disturbance (scorched vs. blowdown forest), snow (present vs. absent) and pre-eruption seral state (clearcut vs. old forest).

The absence of significant variation within zones lends strong support to the results of zonal comparisons (H1 and H2), which could have been biased by uneven replication of site types. Although low replication may limit our ability to detect differences, the result is consistent with previous studies of the blow-down zone, where we expected the greatest variation among site types. Here, rates of change did not differ for many community attributes (total plant cover, richness, diversity and evenness) despite differences in species composition among site types (Cook & Halpern, 2018).

Greater variation among than within zones suggests that after three decades, disturbance severity continues to play a stronger role than do the smaller scale influences of site history and local environment. Nevertheless, our comparisons reveal two unexpected results: (1) surprising similarity in rates of change between primary and secondary successional zones and (2) stronger contrasts between the latter, despite greater similarity of disturbance. Our results underscore the notion that the classic distinction between primary and secondary succession is not sufficient to capture the heterogeneity of disturbance characteristics, site conditions and successional processes initiated by large infrequent disturbances (Turner et al., 1998).

#### 4.4 | Conclusions

We found that severity of volcanic disturbance was a major driver of successional change over a three-decade period, but not in the manner expected. Counter to theory, rates of change were comparably low at both ends of the disturbance gradient and greatest in the middle. These higher rates of change were driven by processes or conditions that were limiting at the extremes of the disturbance gradient. Sites with similar pre- or post-eruption characteristics showed comparable rates of change, but failed to converge compositionally, suggesting strong local controls on succession. Comparative analyses of long-term longitudinal data can provide critical tests of the assumptions and predictions of successional theory.

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#### AUTHORS' CONTRIBUTIONS

C.C.C., J.A.A., A.B., J.E.C., R.d.M., D.G.F., C.B.H., A.H., R.J.P., M.E.S. and D.B.Z. collected or contributed data. C.C.C. conducted the analyses. C.C.C., C.B.H. and J.A.A. led the writing; M.L.A., A.B., J.E.C., R.d.M., D.G.F., A.H., R.J.P., M.E.S. and D.B.Z. provided feedback on one or more drafts. All authors gave final approval for publication.

#### DATA ACCESSIBILITY

Blast zone dataset 1980–2010 was originally published by del Moral (2010) and is available in Ecological Archives E091-152: <https://doi.org/10.6084/m9.figshare.c.3303093.v1> (del Moral, 2016). Tephra zone dataset was originally published in Fischer, Antos, Biswas, and Zobel (2018a) available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j2k54s8> (Fischer et al., 2018b). The dataset in its entirety (including all blast, blowdown and tephra zone data) is published in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d9d83q1> (Chang et al., 2018).

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## SUPPORTING INFORMATION

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