



Burn severity and pre-fire seral state interact to shape vegetation responses to fire in a young, western Cascade Range forest

Charles B. Halpern^{a,*}, Joseph A. Antos^b

^a School of Environmental and Forest Sciences, College of the Environment, University of Washington, Seattle, WA 98195, USA

^b Department of Biology, PO Box 3020, University of Victoria, Victoria, B.C. V8W 3N5, Canada

ARTICLE INFO

Keywords:

Early seral
Fire severity
Forest understory
Functional group
Seral state
Species diversity

ABSTRACT

Wildfire size and frequency are increasing across the western U.S., affecting large areas of young, second-growth forest originating after logging and burning. Despite their prevalence in the western Cascade landscape, we have a poor understanding of how these young stands respond to fire or how their responses differ from older, undisturbed forests, which are well studied. We explore these questions using pre- and early post-fire data from a young (<30-year-old), naturally regenerating forest in western Oregon that was burned preemptively to limit spread of the 2018 Terwilliger Fire. We exploit natural variation in the initial vegetation and fire behavior to test how pre-fire seral state (relative abundance of early-seral vs. forest-generalist species) and burn severity interact to shape short-term responses to fire. Drawing from disturbance theory and studies of fire in older forests we hypothesized that pre-fire seral state would mediate compositional change and functional-group cover and richness through the regenerative and clonal traits of available species. Two years after fire, we found greater compositional change with increasing fire severity, although the effect was weaker where early-seral species dominated prior to burning. Species richness was unaffected by increasing fire severity as gains in early-seral species were balanced by loss of forest species. In contrast, species diversity (Hill's N_1) and evenness declined, reflecting a shift in the dominance structure of the understory, with the pre-fire dominant, *Pteridium aquilinum*, expanding further, and forest generalists declining. Among plant functional groups, both annuals and perennials responded positively to fire severity, but annuals remained sparse (<1% of herbaceous cover), a stark contrast to their dominance after fire in older forests. Increasing fire severity enhanced the cover and richness of early-seral herbs. However, it reduced the cover or richness of most other groups, including early-seral shrubs, forest herbs, and forest shrubs. Within most functional groups, species varied in their responses to fire, reflecting variation in the type and depth of burial of perennating structures and in the potential for clonal growth. Our results underscore the importance of pre-fire conditions for shaping understory responses to fire in young forests, as they do in older forests. Legacies of past disturbance and species' adaptations to fire clearly favor early-seral herbs over residual forest species. Further study is needed to determine whether the recurrence of fire during the early stages of stand development simply resets succession or alters its longer-term trajectory.

1. Introduction

Fire is integral to the structure and dynamics of western North American forests, but the frequency, size, and severity of fires have been increasing with changes in climate, land use, and other human activities (Abatzoglou and Williams, 2016; Abatzoglou et al., 2021; Cansler and McKenzie, 2014; Nagy et al., 2018). Fire severity is a fundamental driver of structural and compositional change (Abella and Fornwalt, 2015; Halpern, 1988; Hollingsworth et al., 2013; Lecomte et al., 2006; Wang and Kembell, 2005). At one extreme, high-severity crown fire can cause

complete mortality of the overstory and near-complete consumption of understory biomass. At the other extreme, low-severity ground fire can result in minor charring of tree boles and only subtle changes in understory abundance (Dunn et al., 2020; Halpern, 1988; Johnston et al., 2019; Wang and Kembell, 2005). Variation in fire severity can manifest at a range of spatial scales within and among stands, reflecting heterogeneity in forest structure and fuel loading, changes in topography, and shifts in weather conditions (Bradstock et al., 2010; Estes et al., 2017; Weatherspoon and Skinner, 1995).

Plant community characteristics at the time of burning can also

* Corresponding author.

E-mail addresses: chalpern@uw.edu (C.B. Halpern), jantos@uvic.ca (J.A. Antos).

<https://doi.org/10.1016/j.foreco.2022.120028>

Received 4 November 2021; Received in revised form 6 January 2022; Accepted 9 January 2022

Available online 21 January 2022

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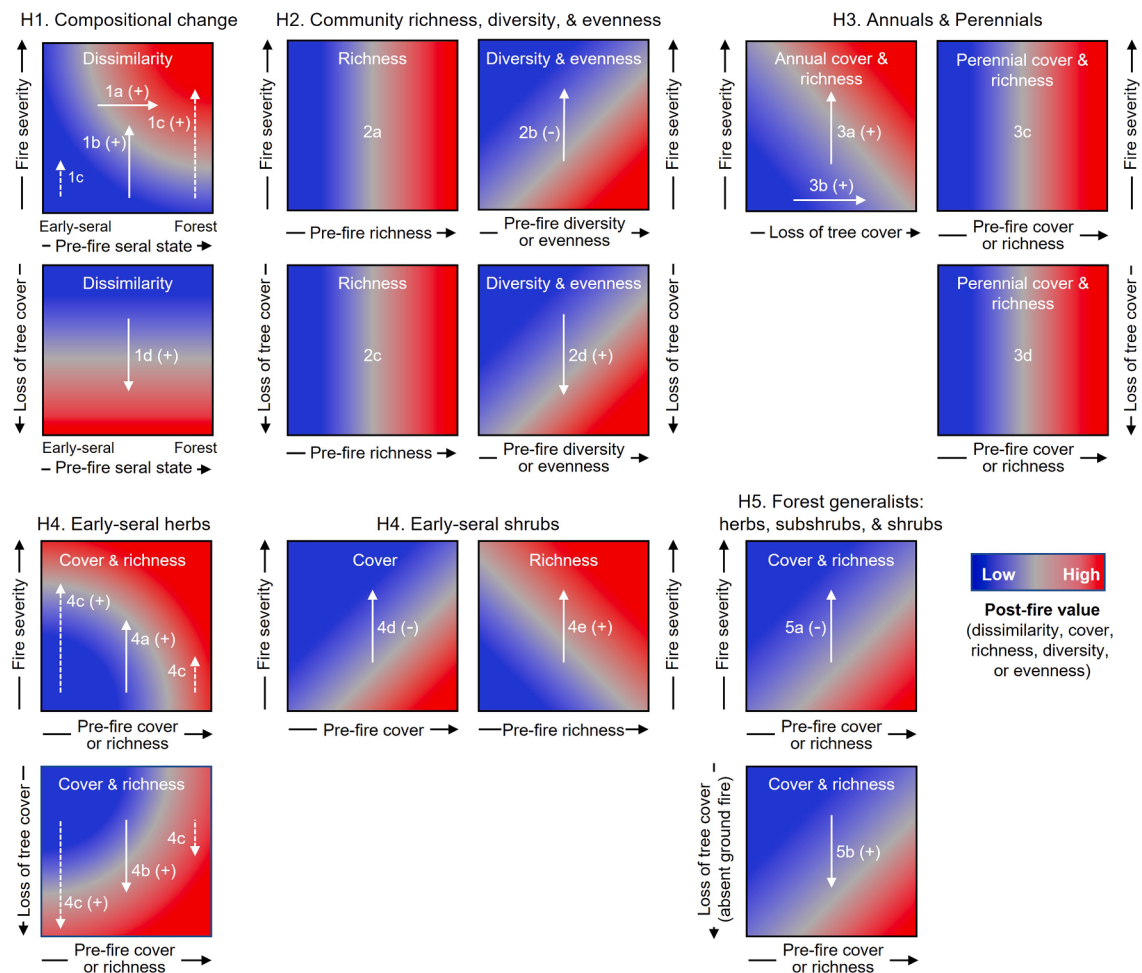


Fig. 1. Hypothesized community and functional-group responses to pre-fire conditions (x axis, except for annuals), fire severity, and loss of tree cover. Colors represent the magnitude of change in species composition from pre- to post-fire (H1) or the post-fire value of the response (H2-H5). Values grade from low (blue) to high (red). Arrows with numbers and lowercase letters correspond to sub-hypotheses in the Introduction and include the sign of the hypothesized relationship (+ or -) with the predictor. Dashed arrows of differing length sharing the same label represent hypothesized interactions, e.g., responses to fire severity or loss of tree cover vary with pre-fire seral state (H1) or pre-fire cover or richness (H4). For H2 through H5, positive correlations between pre- and post-fire values are not shown with horizontal arrows but are implicit in the gradation from blue to red along the x axis. Panels without arrows (2a, 2c, 3c, and 3d) indicate no relationship of the response variable to fire severity or loss of tree cover, but a positive correlation with the pre-fire value.

shape responses to fire through the life-history traits of the available species (Halpern, 1988; Noble and Slatyer, 1980; Pyke et al., 2010; Rowe, 1983). These include mechanisms of persistence through, or recolonization after, fire (e.g., buried meristems or seeds) and traits that facilitate growth in the post-fire environment (e.g., clonal expansion via root systems, rhizomes, or stolons) (Archibold, 1989; Chapman and Crow, 1981; Flinn and Wein, 1977; Grubb, 1988; Halpern, 1989; McLean, 1969). As a result, responses to fire can vary with seral composition, as dominance shifts from disturbance-dependent, shade-intolerant ruderals to disturbance-sensitive, shade-tolerant species. The question of how seral state mediates the response to fire is becoming increasingly important as the size and frequency of wildfires increase across the western U.S. and other regions globally (Bowd et al., 2021; Busby et al., 2020; Donato et al., 2009; Gustafsson et al., 2021; Halofsky et al., 2020; McCord et al., 2019). Recent wildfires in areas west of the Cascade crest in Oregon have been unusually large, burning through centuries-old unmanaged forests, as well as younger stands recovering from recent logging and burning disturbance (Abatzoglou et al., 2021; McEvoy et al., 2021). Low-elevation forests in this region are characterized by a mixed-severity fire regime, with episodic fires of varying size and severity often separated by long fire-free intervals (a century or more; Morrison and Swanson, 1990; Teensma, 1987; Tepley et al., 2013;

Weisberg and Swanson, 2003). As a result, recurrence of fire prior to canopy closure is uncommon (but not unprecedented; Agee, 1993; Gray and Franklin, 1997; Thompson et al., 2007) and is more likely to occur in warmer, drier forests to the south (e.g., the Klamath-Siskiyou region; Donato et al., 2009; Odion et al., 2004; Thompson et al., 2007).

Young forests (<60 years old) managed for timber production dominate the western Cascade landscape, yet studies of understory response to fire have been conducted almost exclusively in older forests subject to logging and broadcast burning (Compagnoni and Halpern, 2009; Dyrness, 1973; Halpern, 1988, 1989; Halpern and Franklin, 1990; Halpern and Spies, 1995; Isaac, 1940; Morris, 1970; Schoonmaker and McKee, 1988; Steen, 1966; but see Kayes et al., 2010). Collectively, these studies suggest a common progression of fire-related declines in the abundance and diversity of characteristic forest species, rapid colonization and growth of disturbance-dependent early-seral annuals and perennials, and gradual replacement of early-seral perennials by forest species. However, they also reveal considerable variation in the rates of decline, colonization, and recovery of these plant groups—variation tied to pre-fire composition and fire severity (Halpern, 1988, 1989; Halpern and Franklin, 1990). How these factors shape responses to fire in younger forests remains unclear, although post-fire outcomes are likely to vary as dominance shifts from early-seral annuals to longer-lived

perennials to residual forest species (Halpern 1989; Halpern and Franklin, 1990; Halpern and Lutz, 2013). For example, recurrence of fire early in succession may have little effect on species composition, simply reinforcing the dominance of early-seral perennials over slowly recovering forest species. In contrast, if fire occurs after canopy closure it is likely to reset succession, as it does in older stands, reducing the abundance and diversity of shade-tolerant forest species and triggering the establishment of disturbance-dependent annuals and perennials. At this stage of forest development, responses are likely to hinge on pre-fire conditions (abundance and diversity of forest species) and fire severity, which jointly affect the nature and magnitude of species decline and recruitment (Halpern, 1989; Halpern and Spies, 1995).

Fire can also influence the understory indirectly, through effects on the overstory. For example, under conditions of patchy burning, smaller diameter trees with characteristically thinner bark may succumb to fire, while the adjacent vegetation remains unburned or is minimally damaged. This fire-induced mortality can lead to increased levels of light and reduced competition for soil resources. Understory species that are able to capitalize on these changing resource conditions (e.g., through clonal growth) may benefit indirectly from burning.

Here, we examine understory responses to fire of varying severity in a young, naturally regenerating forest in western Oregon. The site, which had supported a nearly 30-year study of post-logging succession (Antos et al., 2003; Compagnoni and Halpern, 2009; Halpern et al., 1997), was subjected to a controlled burn in fall 2018 to limit spread of the 4400-ha Terwilliger Fire. At the time of burning, sample plots encompassed a gradient of seral states reflecting the patchy nature of tree regeneration—from treeless openings dominated by early-seral perennials to closed-canopy forests dominated by shade-tolerant shrubs. Fire behavior was also patchy, leaving some plots unburned and others with partial to complete mortality of the overstory. These multiple sources of variation—captured by an established system of vegetation plots—created a model system for examining how pre-fire seral state, burn severity, and changes in the resource environment interact to shape community, functional-group, and species' responses to fire. Drawing from disturbance theory and studies of fire effects in older forests, we posed the following hypotheses, illustrated graphically in Fig. 1.

H1. Compositional change. Compositional change (pre- to post-fire dissimilarity) will increase across the gradient of pre-fire seral states (1a), reflecting greater potential for turnover where forest species dominate. Compositional change will also increase with severity of ground fire (1b), but to a lesser degree where early-seral species dominate (1c). Finally, compositional change will increase with loss of tree cover, independent of fire (1d), as light and soil resources become more available.

H2. Community-level changes in richness, diversity, and evenness. Species richness will be unaffected by severity of ground fire (2a) as recruitment of disturbance-dependent early-seral species is balanced by loss of characteristic forest species (see H4, H5). In contrast, diversity and evenness (which account for the relative abundance of species) will decline with fire severity (2b), as dominance shifts to early-seral species. Richness will be unaffected by loss of tree cover (2c), but diversity and evenness will increase as subordinate species respond positively to increases in resource availability (2d).

H3. Annual vs. perennial herbs. Cover and richness of disturbance-dependent annuals will increase with fire severity (3a) and loss of tree cover (3b). In contrast, cover and richness of the more functionally diverse group of perennial herbs (including both early-seral and forest species) will show little net change with fire severity (3c) or loss of tree cover (3d).

H4. Early-seral species. Early-seral herbs will respond positively to fire severity (4a) and loss of tree cover (4b) but responses will be weaker where pre-fire cover or richness are greater (4c). Cover of early-seral shrubs will decline with fire severity (4d), reflecting dominance of a non-sprouting species, but richness will be enhanced by recruitment of

new species (4e).

H5. Forest generalists. Cover and richness of disturbance-sensitive forest generalists will decline with fire severity (5a). However, in the absence of ground fire, cover and richness will increase with loss of tree cover (5b).

H6. Variation within functional groups. With the exception of annuals, species within functional groups will vary in their responses to fire, reflecting variation in the type and depth of perennating structures and in species' clonal traits.

2. Methods

2.1. Study site and disturbance history

The 4-ha Starrbright study site (named after the original timber sale) lies at 730 m elevation on a gentle, east-facing slope above the south fork of the McKenzie River in the western Cascade Range of Oregon (44° 00' N, 122° 11' W). The surrounding landscape is a patchwork of unmanaged (mature to old-growth) and second-growth forests originating from clearcut logging in the 1970s and 1980s. The climate is Mediterranean, characterized by cool, wet winters and warm, dry summers. At the central meteorological station at the H. J. Andrews Experimental Forest (450 m elevation, 25 km to the north) annual precipitation averages ~2300 mm, but only 6% falls during summer (June through August; Bierlmaier and McKee, 1989). July and January temperatures average 17.8 °C and 0.6 °C, respectively. The soil at Starrbright is a deep (>1.5 m) loamy Andisol (frigid typic Hapludand) derived from weathering of andesite, breccia, and volcanic ash (Antos et al., 2003). Prior to logging, the site supported mature and old-growth forests of *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. The understory was dominated by *Rhododendron macrophyllum*, *Gaultheria shallon*, and *Mahonia nervosa*, evergreen shrubs that are characteristic of warm, dry sites in the *Tsuga heterophylla* zone (Hemstrom et al., 1987). Cover of herbaceous species, including *Trientalis borealis* var. *latifolia*, *Viola sempervirens*, and *Whipplea modesta*, was sparse by comparison.

The site was clearcut logged in early summer 1991 and broadcast burned in fall 1991 in a moderate- to high-intensity fire (Antos et al., 2003). Over the ensuing decades, natural reestablishment of *Pseudotsuga menziesii* was gradual and patchy giving rise to a mosaic of seral states—from treeless openings dominated by early-seral herbs (*Pteridium aquilinum*) or shrubs (*Arctostaphylos columbiana*) to closed-canopy forests dominated by residual forest shrubs. On 5 September 2018 the site was subjected to a controlled burn to limit further spread of the 4400-ha Terwilliger Fire from the north. At the time of burning, minimum relative humidity was ~24–30% and fine-fuel moisture was ~7%. Charring or consumption of litter and duff were highly variable, char heights on tree boles ranged from ~0.3 to 2 m, and tree mortality was patchy (see Section 3.1).

2.2. Experimental and sampling designs

We designed the original experiment in 1990 as a series of species-removal treatments to assess the importance of competition during early succession (Halpern et al., 1997). Each of 25 experimental blocks included a control and eight species-removal treatments. In the latter, species with differing seral roles were removed from a 2.5 × 2.5 m treatment plot. Removals were conducted two to three times per year for 5 years, then annually until the recent fire (2018, year 27). Responses of the target species or the community as a whole were measured in a 1 × 1 m sample plot centered within the treatment plot. Plots were first sampled in 1990, prior to clearcut logging (1991), then annually after broadcast burning (1992). Six treatments were discontinued early in the study as the early-seral target species declined (Halpern et al., 1997). The three remaining treatments (75 plots in total) were maintained and are included in the current study: Control (no removals); removal of *Rubus ursinus* (a subordinate forest subshrub that responds positively to

Table 1

Species' growth forms, longevity, seral roles, clonal potential, method of clonal spread, pre-fire trend, and pre- and post-fire frequency (Freq) and cover. Species present in at least 5 of the 75 plots are shown. Growth form (Gf) and longevity: H_a (herb, annual), H (herb, perennial), Ss (subshrub), S (shrub), or T (tree). Seral role: Es (early-seral), F (forest generalist), or U (unclassified). Clonal potential: 0 (none/weak), + (moderate), or ++ (strong). Trend (trend in cover during the 5 years prior to fire): – (declining), 0 (stable), + (increasing), or a = absent. See [Section 2.3](#) for details on species' assignments to groups and clonal traits.

Species	Gf	Seral role	Clonal potential	Method of spread	Trend	Pre (2018)		Post (2020)	
						Freq (%)	Cover (%)	Freq (%)	Cover (%)
<i>Collomia heterophylla</i>	H _a	Es	0	–	–	6.7	<0.1	42.7	0.1
<i>Lotus unifoliolatus</i>	H _a	Es	0	–	–	9.3	<0.1	14.7	<0.1
<i>Senecio sylvaticus</i>	H _a	Es	0	–	a	0.0	0.0	8.0	<0.1
<i>Leucanthemum vulgare</i>	H	Es	+	rhizome	0	6.7	<0.1	8.0	<0.1
<i>Pseudognaphalium canescens</i>	H	Es	0	–	–	2.7	<0.1	9.3	0.1
<i>Hypericum perforatum</i>	H	Es	+	root	–	10.7	0.3	12.0	0.1
<i>Anaphalis margaritacea</i>	H	Es	+	rhizome	–	8.0	0.1	4.0	<0.1
<i>Elymus glaucus</i>	H	Es	+	rhizome	–	42.7	0.1	26.7	0.1
<i>Lotus crassifolius</i>	H	Es	+	rhizome	–	6.7	0.4	14.7	0.4
<i>Chamerion angustifolium</i>	H	Es	++	root	–	8.0	0.1	42.7	3.1
<i>Pteridium aquilinum</i>	H	Es	++	rhizome	–	80.0	36.3	78.7	45.7
<i>Fragaria vesca</i>	H	Es	++	stolon	–	78.7	1.1	65.3	1.2
<i>Clinopodium douglasii</i>	H	Es	++	stolon	+	6.7	0.4	9.3	0.4
<i>Festuca occidentalis</i>	H	F	0	–	0	8.0	<0.1	8.0	<0.1
<i>Hieracium albiflorum</i>	H	F	0	–	–	26.7	0.2	21.3	0.2
<i>Anemone deltoidea</i>	H	F	+	rhizome	0	12.0	0.6	13.3	0.1
<i>Asarum caudatum</i>	H	F	+	rhizome	+	16.0	1.0	14.7	0.6
<i>Campanula scouleri</i>	H	F	+	rhizome	–	6.7	0.1	8.0	0.2
<i>Galium triflorum</i>	H	F	+	rhizome	–	20.0	0.1	21.3	0.1
<i>Viola sempervirens</i>	H	F	+	stolon	0	57.3	0.7	56.0	0.5
<i>Trientalis borealis</i> ssp. <i>latifolia</i>	H	F	++	rhizome	+	78.7	1.7	76.0	1.8
<i>Lupinus latifolius</i>	H	U	0	taproot	–	21.3	0.3	20.0	0.8
<i>Linnaea borealis</i>	Ss	F	++	stolon	+	13.3	1.0	13.3	1.0
<i>Rubus ursinus</i>	Ss	F	++	stolon	0	96.0	12.1	93.3	11.7
<i>Whipplea modesta</i>	Ss	F	++	stolon	–	34.7	0.8	41.3	0.7
<i>Arctostaphylos columbiana</i>	S	Es	0	–	–	30.7	9.3	22.7	0.8
<i>Rubus parviflorus</i>	S	Es	++	rhizome	0	22.7	1.8	24.0	3.5
<i>Gaultheria shallon</i>	S	F	++	rhizome	+	54.7	8.9	50.7	3.8
<i>Mahonia nervosa</i>	S	F	++	rhizome	+	40.0	6.4	38.7	4.5
<i>Rhododendron macrophyllum</i>	S	F	0	–	0	21.3	8.1	12.0	4.1
<i>Pseudotsuga menziesii</i>	T	F	0	–	+	86.7	63.9	60.0	48.9
<i>Thuja plicata</i>	T	F	0	–	+	18.7	1.0	17.3	0.7
<i>Tsuga heterophylla</i>	T	F	0	–	+	10.7	0.6	9.3	0.1

disturbance; Halpern, 1989); and combined removal of *Gaultheria shallon* and *Mahonia nervosa* (dominant forest shrubs). We account for the history of species' removal from non-control plots by modeling post-fire responses as a function of immediate pre-fire conditions (see [Section 2.5](#)).

Data for this study include both pre- (2018) and post-fire (2019 and 2020) measurements, which were taken during the first week of July. In each plot, cover was visually estimated for each species to the nearest 0.1 or 1% (contingent on cover). For consistency, all estimates were made by a single observer (the primary author). Plant nomenclature follows the USDA Plants Database ([USDA and NRCS, 2021](#)).

In 2019 (year 1) we also recorded four characteristics of the fire in and adjacent to each plot: (1) percentage of ground surface burned within the plot (litter either charred or consumed by fire); (2) percentage of ground surface burned adjacent to the plot (to a distance of 0.5 m); (3) tree mortality (proportion of live trees ≥ 1.4 m tall that died within 2.5 m of the plot perimeter); and (4) change in tree cover above the plot (2019 minus 2018 cover of *P. menziesii*). With one exception, all fire-related tree mortality occurred within the first year. Together, these variables captured the severity of ground fire in and adjacent to the plots and the changing resource conditions associated with loss of tree cover.

2.3. Species' classification (growth form, longevity, seral role) and regenerative traits

To facilitate comparisons with previous work, we assigned species to functional groups based on growth form, longevity, and seral role ([Table 1](#)). Growth forms included herbs (forbs, ferns, and graminoids), subshrubs (trailing species with a woody stem or base), shrubs (erect

woody species), and trees (conifers). Herb species were further classified by longevity, as annual or perennial (irrespective of seral role). Within each growth form (herb, subshrub, and shrub), species were also classified by seral role—early seral or forest generalist—following similar groupings in previous studies (Dyrness, 1973; Halpern, 1989; Halpern and Franklin, 1990; Halpern and Spies, 1995; Schoonmaker and McKee, 1988). Early-seral species (or 'invaders'; Halpern, 1989; Schoonmaker and McKee, 1988) typify disturbed sites and are largely absent from closed-canopy forests. Forest generalists characterize a wide range of forest ages but can survive stand-replacing disturbance (as 'residuals'; Halpern, 1989; Schoonmaker and McKee, 1988). Due to the recency of logging and burning, fire-sensitive late-successional species (Halpern, 1989; Halpern and Spies, 1995) were largely absent from the site and are not considered here. One perennial herb, *Lupinus latifolius*, more typical of meadow habitats, was not assigned a seral role. For each plot $\times$ sampling date, we tallied the number (richness) and summed the cover of species representing each functional group. These plot-level attributes served as the bases for functional-group analyses.

Information on species' regenerative and clonal traits ([Table 1](#))—used to interpret functional-group responses to fire—derives from the following sources: Antos and Halpern, 1997; Haeussler and Coates, 1986; Halpern, 1989; Halpern and Franklin, 1990; Hitchcock et al., 1969; Huffman and Tappeiner, 1997.

2.4. Predictors of vegetation response: pre-fire conditions and fire effects

Our statistical models assess second-year (2020) responses to pre-fire (2018) conditions and to the direct and indirect effects of fire. For measures of cover and diversity (richness, diversity, and evenness),

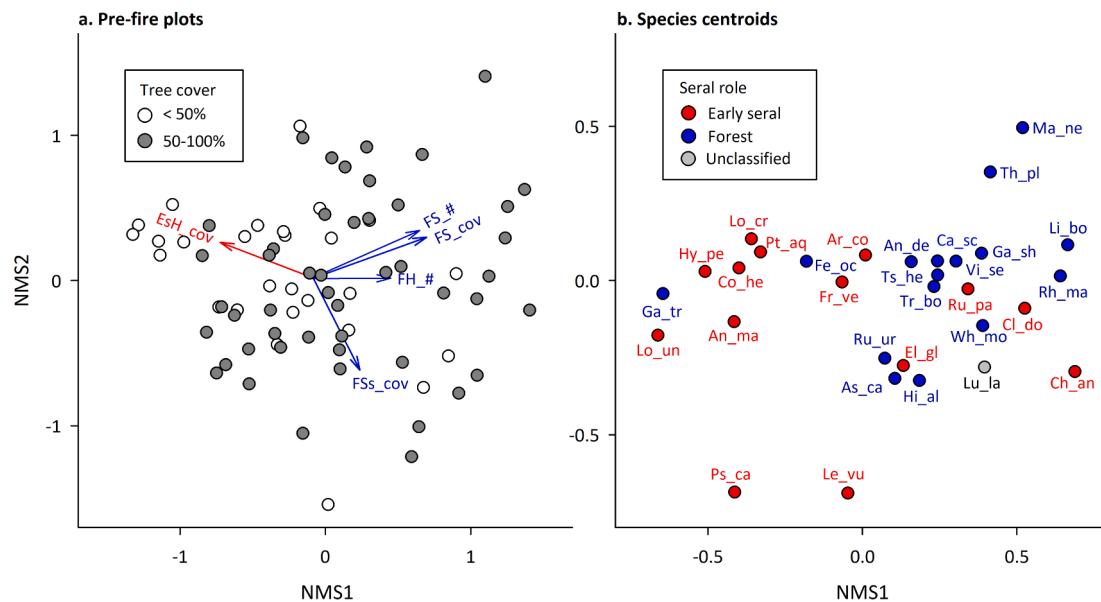


Fig. 2. Non-metric multidimensional scaling (NMS) ordination of species composition prior to fire. (a) Plot scores and axis correlations ($r > 0.5$) with functional-group cover and richness. Plots with $\geq 50\%$ tree cover prior to fire are shaded. NMS1 correlates negatively with cover of early-seral herbs (EsH_cov, -0.73), positively with cover and richness of forest shrubs (FS_cov, 0.69 ; FS_#, 0.66), and positively with richness of forest herbs (FH_#, 0.54). NMS2 correlates negatively with cover of forest subshrubs (Fss_cov, -0.63). (b) Species' centroids and seral coding (red, early-seral species; blue, forest-generalist species; grey, unclassified). Codes correspond to the first two letters of the genus and species name (see Table 1).

models included the corresponding pre-fire value. For compositional change, the pre-fire condition was an index of seral status, represented by the plot score along the first axis (NMS1) of a non-metric multidimensional scaling ordination of the 2018 cover data. Rare species (present in < 5 plots) were excluded, as was the dominant tree species, *Pseudotsuga menziesii*, because it was used to characterize the effects of fire (see Section 2.2). Cover was square-root transformed to reduce the influence of dominant species. The analysis was conducted in PC-ORD ver. 7.0 (McCune and Mefford, 2016) using the 'slow and thorough' autopilot setting, Sorensen (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). NMS1 captured the natural progression in dominance from early-seral to forest species, while accounting for species' removals from non-control plots (Section 2.2).

We used principal components analysis, PCA, to reduce the fire-effects variables to a smaller number of model predictors. Four variables were included: percentage of ground surface burned (1) within and (2) adjacent to the plot, (3) proportion of trees dying (mortality), and (4) pre- to post-fire change in tree cover (almost entirely *P. menziesii*). Imputed values of mortality were generated for 10 plots that lacked trees. Plots scores along the first two principal components served as proxies for severity of ground fire (PCA1) and loss of tree cover (PCA2) (see Section 3.1). PCA was conducted in JMP Pro 15.2.0 (SAS, 2019).

2.5. Measures and models of community, functional-group, and species-level response

We used standard least-squares regression of plot-scale data to assess (1) community, (2) functional-group, and (3) species-level responses to fire. We considered four community metrics: compositional change and three measures or components of diversity: species richness, diversity, and evenness in 2020. Compositional change, the Bray-Curtis dissimilarity between each pre- (2018) and post-fire (2020) plot, was computed from a matrix of square-root transformed cover values after dropping rare species (present in < 5 plots). Richness was expressed as the total number of species/1-m² plot. Diversity was computed as Hill's N_1 (Hill, 1973), the exponential of Shannon's index:

$$N_1 = \exp - \sum p_i \ln p_i$$

where p_i is the proportional abundance of the i^{th} species within the plot. N_1 shares the same units and scale as richness (Hill's N_0), but reduces the relative importance of rarer taxa. It is often described as the effective number of species or the equivalent number of equally common species (Alatalo and Alatalo, 1977; Hill, 1973; Jost, 2006; Peet, 1974). Evenness (E) was computed as Alatalo's (1981) modification of the Hill ratio, N_2/N_1 :

$$E = (N_2 - 1)/(N_1 - 1)$$

where N_2 is the reciprocal of Simpson's index ($1/\sum p_i^2$). Ranging from 0 to 1, evenness represents the ratio of 'very abundant' to 'abundant' species.

Functional-group responses included year 2 (2020) cover or richness of each growth form (herbs, subshrubs, or shrubs) or combination of growth form and seral group (e.g., early-seral herbs, early-seral shrubs, forest herbs, etc.). We also modeled the second-year cover of species within each functional group, provided they were present in at least 10 plots prior to or after the fire. In each regression model, we included the relevant pre-fire term (plot score along NMS1 or pre-fire cover, richness, diversity, or evenness) and the two fire-effects terms—plot scores along PCA1 and PCA2 (proxies for severity of ground fire and loss of tree cover, respectively). Models included all two-way interactions but not the three-way interaction which was subsumed by the error term. All models accounted for species' removals from non-control plots because they incorporated pre-fire conditions implicitly (pre- to post-fire dissimilarity) or explicitly (pre-fire cover, richness, diversity, or evenness).

To achieve normality of residuals, response data were square-root or log-transformed as necessary. To assess possible collinearity among predictors, we examined variance inflation factors (VIFs) of model coefficients, which rarely exceeded 2.5. Graphically, we display model results as a series of contour plots illustrating responses to the relevant pre-fire condition (typically the x axis), severity of ground fire (PCA1), and loss of tree cover (PCA2). All regression models and diagnostic tests were run in JMP Pro 15.2.0 (SAS, 2019).

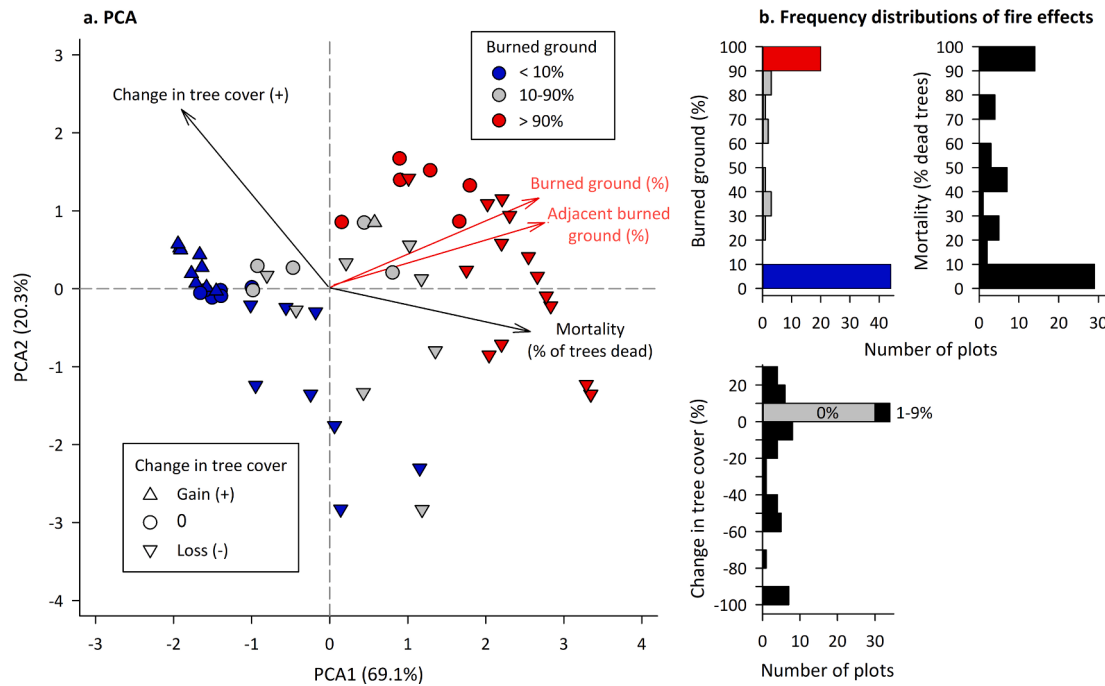


Fig. 3. (a) Principal components analysis (PCA) of fire-effects variables. Arrows represent variable correlations with axes. PCA1, which explains 69.1% of the total variation, is positively correlated with cover of burned ground in and adjacent to the plot ($r = 0.89$ and 0.93 , respectively) and with tree mortality (% of trees dying within 2.5 m of the plot; $r = 0.85$). PCA2 explains 20.3% of the variation, with lower scores corresponding to greater loss of tree cover ($r = 0.74$). Colors correspond to cover of burned ground and symbols correspond to the direction of change in tree cover (loss, no change, or gain). (b) Frequency distributions of fire-effects variables. Among the 75 plots, 30 had no change in tree cover (grey bar).

Table 2

Mean (SD) cover and richness of plant functional groups prior to (Pre) and two years after fire (Post) ($n = 75$ plots). Change is Post minus Pre. P values are based on Wilcoxon signed-rank tests comparing the median change to zero. Bold indicates a significant change ($P \leq 0.05$); underscore indicates marginal significance ($0.05 < P \leq 0.10$).

Functional group	Cover (%)					Richness (species/1-m ² plot)				
	Pre (SD)	Post (SD)	Change	P		Pre (SD)	Post (SD)	Change	P	
Total herbs	44.1 (35.2)	56.1 (38.4)	+12.0	0.0003		5.5 (1.9)	6.2 (2.4)	+0.7	0.003	
Annual herbs	0.1 (0.7)	0.2 (0.4)	+0.1	<0.0001		0.3 (0.6)	0.9 (0.9)	+0.6	<0.0001	
Perennial herbs	43.8 (35.1)	55.7 (38.3)	+11.9	0.0003		4.7 (1.5)	4.9 (1.8)	+0.2	<u>0.089</u>	
Early-seral herbs	39.0 (36.3)	51.3 (40.0)	+12.3	0.0003		2.4 (1.3)	3.4 (1.8)	+0.9	<0.0001	
Forest-generalist herbs	4.7 (6.5)	3.8 (4.5)	-0.9	0.175		2.3 (1.1)	2.2 (1.3)	-0.1	0.161	
Forest subshrubs	13.9 (17.2)	13.4 (16.5)	-0.5	0.710		1.5 (0.7)	1.5 (0.7)	+0.01	0.587	
Total shrubs	36.1 (39.8)	17.4 (29.4)	-18.7	<0.0001		1.8 (1.4)	1.6 (1.3)	-0.2	<u>0.060</u>	
Early-seral shrubs	11.4 (22.6)	4.4 (13.0)	-7.0	0.008		0.9 (0.6)	0.9 (0.8)	-0.04	0.575	
Forest-generalist shrubs	24.7 (35.5)	13.0 (27.3)	-11.7	<0.0001		1.2 (1.1)	1.0 (1.0)	-0.2	0.019	

3. Results

3.1. Variation in pre-fire conditions and fire effects

Compositionally, plots spanned a gradient of seral states prior to burning, reflecting a shift in dominance from early-seral herbs to forest shrubs (left to right along NMS1; Fig. 2a and b). Correlations with NMS1 were negative for early-seral shrub cover ($r = -0.73$) but positive with forest herb and shrub cover or richness ($r = 0.54$ – 0.69) (Fig. 2a). Among plots, early-seral herbs showed greater variation in cover (0.2–126%) and richness (1–8 species/1-m² plot) than did forest herbs (0–43.5% cover, 0–5 species/plot). Despite a sizeable species pool (14), annuals contributed minimally to herbaceous cover or richness (means of 0.1% and 0.3 species/plot). Forest shrubs showed greater variation in cover (0–145%) than did early-seral shrubs (0–95%), but both groups comprised a small number of species (Table 1).

The nature and severity of fire effects also varied widely among plots. Reduction of the fire-effects data with principal components analysis

yielded a first and second principal component explaining 69.1 and 20.3% of the total variation in the data (Fig. 3a). PCA1 was highly correlated with cover of burned ground in and adjacent to the plot ($r = 0.89$ and 0.93 ; range of 0–100%) and with tree mortality ($r = 0.85$; range of 0–100%; Fig. 3b). PCA2 was correlated with change in tree cover ($r = 0.74$); lower scores corresponded to greater loss of tree cover (as high as 100 percentage points); higher scores corresponded to no change or a small increase in cover (0 to +25 percentage points; Fig. 3b). For simplicity we refer to PCA1 and PCA2 as indices of ground-fire severity and loss of tree cover, respectively.

3.2. Site-level changes in growth form and functional-group cover and richness

For the site as whole, fire had stronger effects on functional-group cover than on richness (Table 2). On average, herb cover increased by 27% (from 44.1% prior to fire to 56.1% two years after fire; Table 2), driven by growth of early-seral perennials. Over the same period, shrub

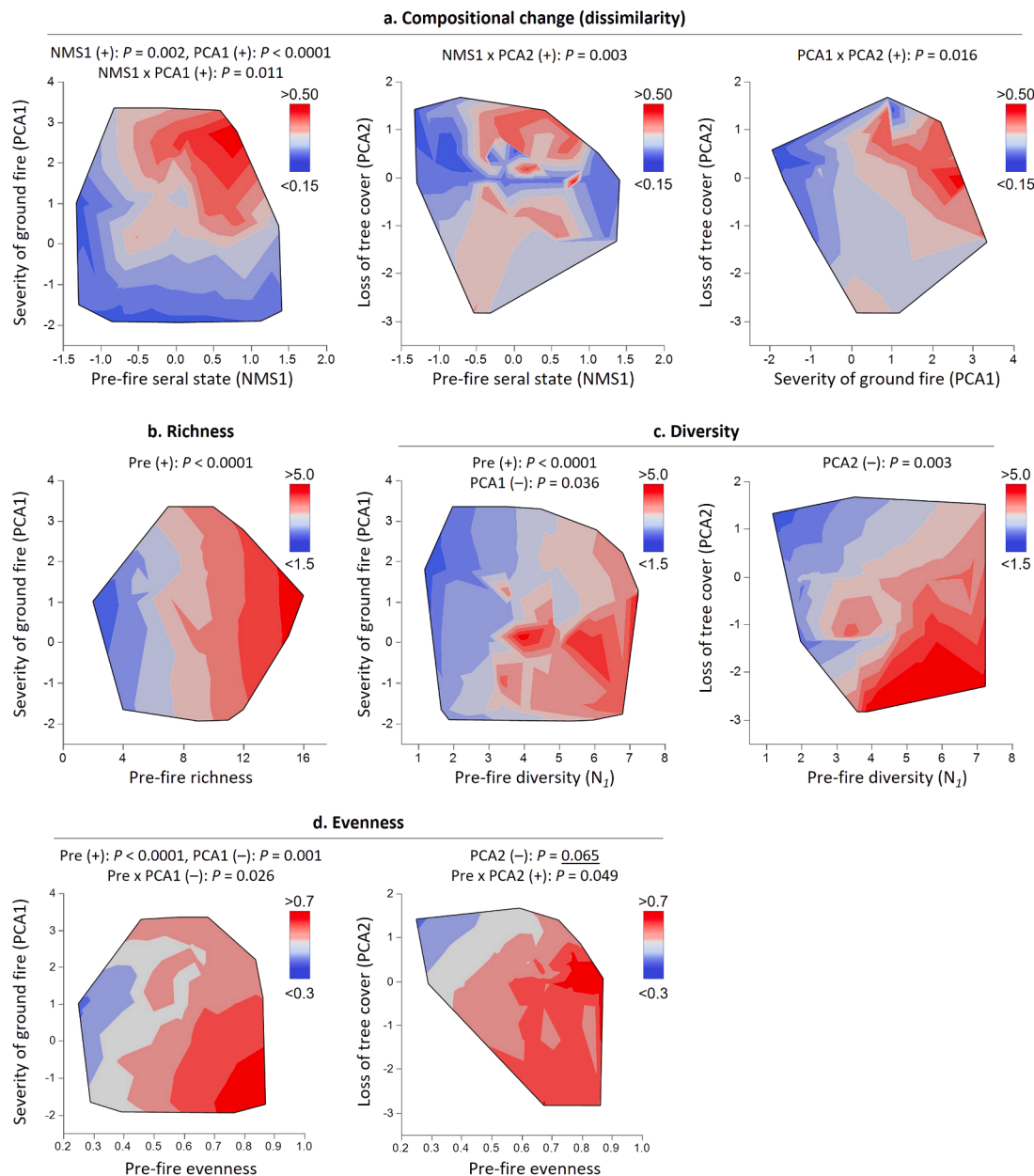


Fig. 4. Modeled relationships of community-level metrics in year 2 to pre-fire conditions (Pre), PCA1 (proxy for severity of ground fire), and PCA2 (proxy for loss of tree cover), with lower scores corresponding to greater loss of cover). Predicted values are plotted, increasing in magnitude from blue to red. The signs (+ or -) and significance of model terms, including interactions, are shown above each panel. Table 3 contains full model results. (a) Compositional change (Bray-Curtis dissimilarity pre- to post-fire), (b) species richness (number of species/1-m² plot), (c) species diversity (Hill's N_I , the exponential of Shannon's index), and (d) species evenness (the modified Hill's ratio, $[N_{2-1}]/[N_{1-1}]$).

cover was greatly reduced (from 36.1 to 17.4%; Table 2) reflecting declines in both early-seral and forest shrubs. Effects on richness were more subtle, including small increases in the number of annual and early-seral herbs (means of 0.6 and 0.9 species/1-m² plot, respectively) and a small decline in the number of forest shrubs (mean of 0.2 species/plot) (Table 2).

3.3. Community-level responses (H1, H2)

We hypothesized that compositional change (pre- to post-fire dissimilarity) would increase across the gradient of pre-fire seral states and as fire severity and loss of tree cover increased (Fig. 1). Further, we expected a weaker response to fire severity where early-seral species dominated. Significant main effects and interactions of NMS1 (pre-fire

seral state) with PCA1 (fire severity) were consistent with these predictions (Fig. 4a, Table 3). However, the relationship to loss of tree cover (PCA2) was not. Instead, it was contingent on pre-fire seral state and fire severity (significant interactions of PCA2 with NMS1 and PCA1; Fig. 4a, Table 3).

Among measures of diversity, year 2 responses to fire severity and changes in tree cover were largely consistent with predictions. Richness was unaffected by fire severity but highly correlated with pre-fire richness (Fig. 4b, Table 3). Diversity declined with increasing fire severity (Fig. 4c, Table 3), as did evenness, although the decline in evenness was contingent on pre-fire conditions (marginally significant Pre x PCA1 interaction; Fig. 4d, Table 3). Richness was unaffected by loss of tree cover but diversity and evenness increased (negative correlations with PCA2; Fig. 4c and d, Table 3).

Table 3

Results of regression models of community and functional-group responses two years after fire. Data transformation (Trans), adjusted R^2 for the full model, and sign (+ or –) and significance (P) of model terms are shown ($n = 75$ for all models). Underscore indicates marginal significance ($0.05 < P \leq 0.10$) and blank cells indicate non-significance of model terms. 'Pre' is the pre-fire value or, for compositional change, plot score along NMS1 (a proxy for pre-fire seral state; see Fig. 2a). PCA1 and PCA2 are proxies for severity of ground fire and loss of tree cover, respectively (see Fig. 3a). Data transformation: — (none), sqrt (square root), or log (log [$\times + 1$]).

			Sign (+/–) and significance (<i>P</i>) of model terms											
Response variable	Trans	Adj. <i>R</i> ²	Pre		PCA1		PCA2		Pre × PCA1		Pre × PCA2		PCA1 × PCA2	
Community characteristics														
Compositional change	sqrt	0.54	+	0.002	+	<0.0001			+	0.011	+	0.003	+	0.016
Species richness, <i>N</i> ₀	—	0.56	+	<0.0001										
Species diversity, <i>N</i> ₁	log	0.36	+	<0.0001	–	0.036	–	0.003						
Species evenness, <i>E</i>	—	0.39	+	<0.0001	–	0.001	–	0.026	–	<u>0.065</u>	+	0.049		
Annual vs. perennial herbs														
Annual cover	sqrt	0.42			+	0.004								
Annual richness	sqrt	0.14	+	0.039	+	<0.0001								
Perennial cover	sqrt	0.64	+	<0.0001	+	<0.0001								
Perennial richness	sqrt	0.53	+	<0.0001										
Early-seral groups														
Herb cover	sqrt	0.64	+	<0.0001	+	<0.0001								
Herb richness	sqrt	0.43	+	<0.0001	+	<0.0001								
Shrub cover	log	0.51	+	<0.0001			–	0.011	–	0.030	–	0.001		
Shrub richness	—	0.26	+	<0.0001										
Forest-generalist groups														
Herb cover	sqrt	0.67	+	<0.0001	–	<0.0001	–	0.001			–	0.001		
Herb richness	sqrt	0.65	+	<0.0001	–	0.0001								
Subshrub cover	sqrt	0.81	+	<0.0001			–	0.002						
Subshrub richness	sqrt	0.77	+	<0.0001					–	0.015				
Shrub cover	sqrt	0.87	+	<0.0001	–	<0.0001			–	<0.0001				
Shrub richness	—	0.75	+	<0.0001	–	0.0004			–	<u>0.051</u>				

3.4. Functional-group responses (H3-H5)

For nearly all functional groups, pre-fire cover and richness (Pre) were significant predictors of post-fire response; annual-herb cover was the exception (Table 3). Although annuals responded predictably to fire severity, they accounted for less than 1% of herb cover and fewer than 15% of herb species. Counter to expectation, perennial-herb cover increased with fire severity, although richness was unaffected (Table 3).

As predicted, early-seral herbs responded positively to fire severity, but the increase was not constrained by pre-fire values (non-significant Pre $\times$ PCA1 interactions; Fig. 5a and b; Table 3). In contrast, early-seral herbs did not respond positively to loss of tree cover (Table 3). For early-seral shrubs, the relationship to fire severity was complex (significant Pre $\times$ PCA1 interaction; Fig. 5c, Table 3), reflecting the divergent responses of a fire-sensitive and fire-insensitive species (*Arctostaphylos columbiana* and *Rubus parviflorus*, respectively; see Section 3.5). Counter to expectation, richness of early-seral shrubs was not enhanced by higher severity fire (Fig. 5d, Table 3).

Cover and richness of forest herbs and shrubs declined with fire severity, as predicted (Fig. 6, Table 3). Moreover, for shrubs, the decline in cover was proportional to initial cover (significant Pre $\times$ PCA1 interaction; Fig. 6e, Table 3). Cover of subshrubs (dominated by *Rubus ursinus*) was unaffected by fire severity, but richness was reduced where pre-fire richness was higher (significant Pre $\times$ PCA1 interaction; Fig. 6d, Table 3). In the absence of ground fire we expected forest species to benefit from reductions in tree cover (PCA2), but we saw no evidence of this interaction (Table 3). Rather responses to loss of tree cover varied from consistently positive (subshrubs), to positive contingent on pre-fire cover (herbs), to neutral (shrubs) (Fig. 6, Table 3).

3.5. Species variation within functional groups (H6)

We observed considerable variation in species' responses to fire within functional groups. Among annuals, *Lotus unifoliolatus* responded positively to fire severity (Fig. A1a, Appendix A; Table 4) but colonized few plots, increasing in frequency from 9 to 15% (Table 1). In contrast, *Collomia heterophylla* responded positively to loss of tree cover (Fig. A1b,

Appendix A; Table 4) but colonized many plots, increasing in frequency from 7 to 43% (Table 1).

Among early-seral perennial herbs, responses to fire were consistent with species' life-history and regenerative traits. *Chamerion angustifolium* responded positively to fire severity (Fig. A1c, Appendix A; Table 4), increasing five-fold in frequency in year 1 (from 8 to 43%) and more than an order of magnitude in cover in year 2 (from 0.1 to 3%; Table 1)—trends consistent with a dual strategy of recruitment from seed and vigorous clonal expansion by root systems. *Pteridium aquilinum* also responded positively to fire severity (Fig. A1d, Appendix A; Table 4). Its high frequency prior to fire remained unchanged (~80%), but cover increased from 36 to 46% (Table 1)—trends consistent with a well-protected system of rhizomes and renewal buds. In contrast, *Fragaria vesca* responded negatively to fire severity but positively to loss of tree cover (Fig. A1e, Appendix A; Table 4)—trends consistent with a stoloniferous growth form. Frequency declined from 79 to 65% but cover remained stable (Table 1), as loss from high-severity plots was offset by growth in low-severity plots.

Among forest herbs and subshrubs, responses to fire were also consistent with the type and location of perennating structures. Species regenerating from a shallow caudex (*Hieracium albiflorum*) or surficial stolons (*Viola sempervirens* and *Whipplea modesta*) responded negatively to fire severity (Fig. A2a-c, Appendix A; Table 4). In contrast, species with tubers (*Trientalis borealis* var. *latifolia*) or taproots (*Rubus ursinus*) were unaffected (Fig. A2f and g, Appendix A; Table 4). Responses to loss of tree cover were largely consistent with species' clonal traits. Of four species responding positively to loss of tree cover, three were strongly clonal, spreading by rhizomes (*T. borealis* var. *latifolia*) or stolons (*W. modesta* and *R. ursinus*) (Fig. A2c, f, and g, Appendix A; Table 4).

Early-seral shrubs comprised a small group of species with contrasting responses to fire. *Arctostaphylos columbiana*, a non-sprouting obligate seeder, was highly sensitive to fire: cover declined to near zero in all but unburned plots (significant Pre $\times$ PCA1 interaction; Fig. A1f, Appendix A; Table 4). Although average cover was reduced more than ten-fold, the decline in frequency was moderated by recruitment from the seed bank (Table 1). In contrast, *Rubus parviflorus*, resprouting from a system of deeply buried rhizomes, was unaffected by

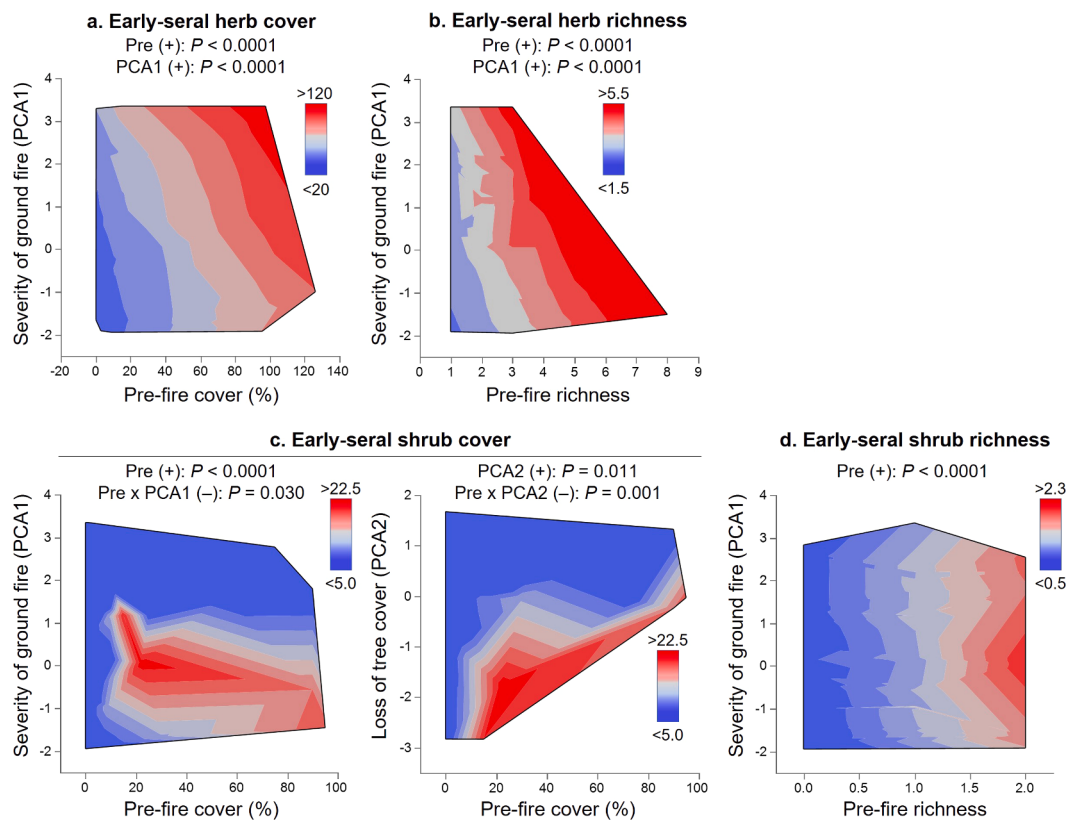


Fig. 5. Modeled relationships of post-fire (year 2) cover and richness of (a, b) early-seral herbs and (c, d) early-seral shrubs to pre-fire cover or richness (Pre), severity of ground fire (PCA1), and loss of tree cover (PCA2). See Fig. 4 for other details.

fire severity (Fig. A1g, Appendix A; Table 4). Frequency remained unchanged and average cover nearly doubled (Table 1).

The three primary forest shrubs, *Gaultheria shallon*, *Mahonia nervosa*, and *Rhododendron macrophyllum*—all sclerophyllous evergreen species—responded negatively to fire severity (Fig. A2d and e, Appendix A; Table 4). Although top-kill reduced the cover of all three species, only *R. macrophyllum*, perennating from a shallow root crown, had substantial mortality (44% reduction in frequency; Table 1). By contrast rhizomatous species, *G. shallon* and *M. nervosa*, showed little change in frequency (Table 1).

4. Discussion

Wildfire frequency, size, and severity are increasing across the western U.S., affecting large areas of natural and managed forests (Abatzoglou et al., 2021; Higuera and Abatzoglou, 2021; Nagy et al., 2018). How seral state at the time of burning influences the response to fire remains poorly understood—limited by the dearth of studies in young forests of known pre-fire structure and composition. We explore this question, capitalizing on pre-fire data from a mosaic of seral states in a young, naturally regenerating forest subjected to a controlled burn of varying severity. Initial changes in community structure supported many of our predictions, underscoring the role of pre-fire seral state in mediating the response to fire severity. They also illustrate how the post-fire dynamics of younger forests may differ from those of older forests, reflecting legacies of past disturbance and the pre-fire dominance of disturbance-adapted early-seral perennials.

4.1. Community-level changes

As predicted, compositional change increased with fire severity. Moreover, the magnitude of change was reduced where early-seral species dominated prior to fire. That said, the shift to early-seral

dominance was driven by perennials, not annuals. Annuals accounted for < 1% of herbaceous cover in year 2—a marked contrast to their typical post-fire dominance (Dyrness, 1973; Halpern, 1988, 1989; Yerkes, 1958). For example, cover of annuals exceeded 40% two years after logging and broadcast burning of older forests at Starrbright and the Andrews Experimental Forest (Compagnoni and Halpern, 2009; Halpern, 1988, 1989). Rapid expansion of the principal species, *Senecio sylvaticus* and *Epilobium brachycarpum*, reflects a combination of traits: long-distance dispersal, maintenance of a seed bank, a preference for burned microsites, and a winter-annual life cycle leading to copious seed production by first-year recruits (Clark, 1991; Halpern, 1989; Halpern et al., 1997, 1999; Harmon and Franklin, 1995; Kellman, 1974; West and Chilcote, 1968). Given the potential for long-distance dispersal and the comparable fall burning of young and older forests, we conclude that the poor development of annuals in this study likely reflects microsite rather than seed limitations (Eriksson and Ehrlén, 1992; Myers and Harms, 2009; Nathan and Muller-Landau, 2000). The controlled fire was cooler and patchier, exposing less mineral soil (5%) than the original broadcast burn (~40%) which was fueled by logging slash. As a result, germination may have been limited by the availability of safe sites (Harper et al., 1961). *Pteridium aquilinum*, which dominated post-fire, may also have inhibited germination. Dense production of litter by *P. aquilinum* poses a physical barrier to the emergence of light-seeded annual species (Gliessman and Muller, 1978; Jatoba et al., 2016). Chemical exudates from its litter or roots can also suppress germination, although the strength of this effect has been debated (del Moral and Cates, 1971; Gliessman, 1976; Haeussler and Coates, 1986; Stewart, 1978). In contrast, the absence of *P. aquilinum* or other early-seral perennials from older forests gives annuals an early post-fire advantage.

We also hypothesized that compositional change would increase with loss of tree cover (declining scores on PCA2)—a response to changing resource conditions (Li et al., 2021; Riegel et al., 1992; Sprugel et al., 2009; Thomas et al., 1999). However, patterns ran counter to

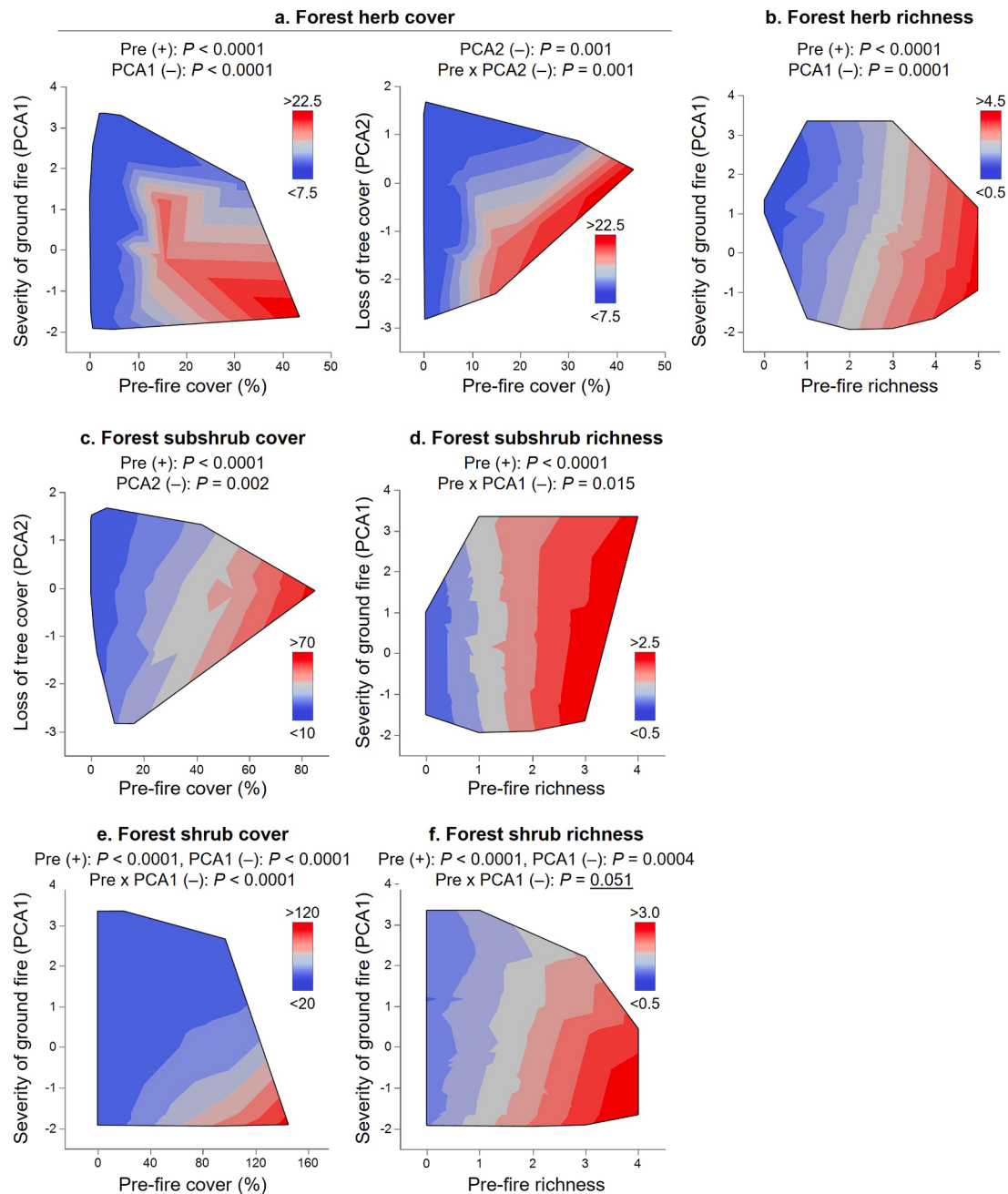


Fig. 6. Modeled relationships of post-fire (year 2) cover and richness of (a, b) forest herbs, (c, d) forest subshrubs, and (e, f) forest shrubs to pre-fire cover or richness (Pre), severity of ground fire (PCA1), and loss of tree cover (PCA2). Marginal significance ($0.05 < P \leq 0.10$) is noted by an underscore. See Fig. 4 for other details.

expectation: compositional change peaked where there was little or no change in tree cover, contingent on pre-fire seral state and fire severity. This counterintuitive result reveals a potential limitation of PCA2 as a proxy for loss of tree cover. Although low scores on PCA2 corresponded to plots with significant loss of tree cover (and presumably large changes in resource availability), higher scores on PCA2 represented two contrasting conditions: plots with little or no loss of tree cover (with presumably minimal resource enhancement) and plots devoid of trees (with unknown changes in resource conditions). It was among the latter—treeless plots dominated by fire-sensitive *Arctostaphylos*

columbiana—that we observed some of the largest changes in species composition.

For the remaining community attributes—species richness, diversity, and evenness—pre-fire conditions predicted post-fire responses, illustrating strong continuity of community structure through fire. However, the relationship to fire severity differed among these metrics. Increasing severity had no effect on richness despite causing significant turnover in the number of early-seral and forest species. Diversity and evenness, which are sensitive to species' abundance, declined with fire severity, reflecting a shift in community structure toward greater dominance by

Table 4

Results of regression models of species' cover two years after fire. Species with asterisks (*) are presented graphically in Fig. A1 or A2 (Appendix A). n = number of plots with the species present. Data transformation (Trans), adjusted R^2 for the full model, and sign (+ or −) and significance (P) of model terms are shown. Underscore indicates marginal significance ($0.05 < P \leq 0.10$) and blank cells indicate non-significance of model terms. Periods (...) indicate interaction terms that were dropped from the model to reduce collinearity. 'Pre' is pre-fire cover. PCA1 and PCA2 are proxies for severity of ground fire and loss of tree cover, respectively (see Fig. 3a). Seral role: Es (early seral) or F (forest). Clonal potential (see Table 1): 0 (none/weak), + (moderate), or ++ (strong). Data transformation: — (none), sqrt (square root), log (log [$\times + 1$]).

Species	Seral role	Clonal potential	n	Trans	Adj. R ²	Sign (+/ −) and significance (P) of model terms									
						Pre	PCA1		PCA2		Pre × PCA1	Pre × PCA2		PCA1 × PCA2	
Annual herbs															
<i>Collomia heterophylla</i> *	Es	0	32	log	0.24					−	0.003	...	...	+	0.022
<i>Lotus unifoliolatus</i> *	Es	0	12	—	0.35			+	0.031			...	...		
Perennial herbs															
<i>Chamerion angustifolium</i> *	Es	++	33	log	0.32			+	0.0003						
<i>Pragaria vesca</i> *	Es	++	61	sqrt	0.43	+	0.007	−	0.0002	−	0.001				
<i>Lotus crassifolius</i>	Es	+	12	log	0.52	+	0.025	+	<u>0.076</u>			...	...		
<i>Pteridium aquilinum</i> *	Es	++	62	—	0.55	+	<0.0001	+	0.0003	+	<u>0.089</u>				
<i>Anemone deltoidea</i>	F	+	11	sqrt	0.93	+	0.001			−	0.030		−	0.004	
<i>Asarum caudatum</i>	F	+	15	sqrt	0.78	+	0.001	−	<u>0.086</u>						
<i>Galium triflorum</i>	F	+	22	sqrt	0.24							+	0.007		
<i>Hieracium albiflorum</i> *	F	0	24	sqrt	0.32	+	<u>0.063</u>	−	0.018			−	<u>0.087</u>		
<i>Trientalis borealis</i> ssp. <i>latifolia</i> *	F	++	60	sqrt	0.51	+	<0.0001			−	0.026				
<i>Viola sempervirens</i> *	F	+	48	sqrt	0.71	+	<0.0001	−	<0.0001			−	0.013		0.003
Subshrubs															
<i>Linnaea borealis</i>	F	++	11	sqrt	0.07										
<i>Rubus ursinus</i> *	F	++	72	sqrt	0.80	+	<0.0001			−	0.006				
<i>Whipplea modesta</i> *	F	++	33	sqrt	0.72	+	<0.0001	−	0.035	−	0.044	−	0.010		
Shrubs															
<i>Arctostaphylos columbiana</i> *	Es	0	29	sqrt	0.30							−	0.017		
<i>Rubus parviflorus</i> *	Es	++	18	log	0.67	+	0.001								
<i>Gaultheria shallon</i> *	F	++	46	sqrt	0.64	+	<0.0001	−	<0.0001			−	0.005		
<i>Mahonia nervosa</i> *	F	++	30	sqrt	0.87	+	<0.0001	−	<0.0001			−	0.001		
<i>Rhododendron macrophyllum</i>	F	0	17	sqrt	0.81	+	0.001	−	0.019	+	<u>0.051</u>	−	0.036		

early-seral *P. aquilinum* and loss of fire-sensitive forest species. Interestingly, fire-related declines in tree cover had the opposite effect, enhancing local diversity and evenness, suggesting that resource addition benefited subordinate over dominant species. This result runs counter to the more common response to resource enrichment in which taller, more competitive species displace shorter, subordinate species (Goldberg and Miller, 1990; Huston, 1979; Tilman, 1984). Results of individual species models also support this interpretation: many common, subordinate herbs and subshrubs responded positively to loss of tree cover, but pre-fire dominants (e.g., *P. aquilinum*) did not. In sum, fire severity had little effect on plot-scale richness, but strong effects on community attributes that are sensitive to the composition or relative abundance of species. Variation in the pre-fire distributions and dynamics of plant functional groups offer insight into these community-level changes.

4.2. Variation among and within functional groups

We expected annuals to respond positively to increasing fire severity and loss of tree cover—conditions that lead to greater exposure of mineral soil and increased levels of light (Dodson et al., 2007; Halpern, 1988; Rossman et al., 2018; Webster and Halpern, 2010; West and Chilcote, 1968). Annual cover and richness increased, but species differed in their relationships to fire: *Lotus unifoliolatus* benefited from higher severity fire, whereas *Collomia heterophylla* benefited from greater loss of tree cover. As with other fire-dependent groups, establishment of annuals may be a direct response to burning (triggered by heating of the soil) or an indirect effect of changing resource conditions (e.g., increasing light or mineral N; Keeley and Fotheringham, 2000; Luna and Moreno, 2009; Pons, 2000). However, we did not expect post-fire richness of annuals to be correlated with pre-fire richness, a pattern more typical of long-lived perennials. Instead, we expected a diffuse seed rain of wind-dispersed species (e.g., *Senecio sylvaticus* and *Epilobium brachycarpum*) to obscure any pre-fire variation. Instead, short-distance dispersers were more prevalent (e.g., *C. heterophylla* and *L. unifoliolatus*) ensuring greater spatial stability of annual richness (Cardina et al., 1996; Colbach et al., 2000; Heijting et al., 2007). It is also possible that the correlation with pre-fire richness stems from temporal continuity of microsite conditions: plots that were favorable to annual establishment prior to burning may have remained more favorable afterwards.

As observed in other systems, we expected wide variation in species' responses to fire to produce little net change in perennial-herb richness or cover (Abella and Springer, 2015; Kerns et al., 2006; Rossman et al., 2018; Webster and Halpern, 2010; Willms et al., 2017). As predicted, perennial richness was unaffected by fire severity, as colonization by early-seral species was balanced by loss of forest species. However, perennial-herb cover increased with fire severity, driven by expansion of the pre-fire dominant, *P. aquilinum*. Protected by a system of deeply buried rhizomes and dormant buds (Cody and Crompton, 1975), *P. aquilinum* is capable of rapid growth after fire (Fletcher and Kirkwood, 1979; Haeussler and Coates, 1986; Isaac, 1940). Although cover of forest herbs declined, low pre-fire abundance constrained the magnitude of loss. Perennial-herb cover may show a different post-fire dynamic where forest herbs are more abundant and the potential for loss of cover is greater.

We expected early-seral herbs to respond positively to increasing severity of fire, assuming that initial cover and richness were not limiting. Cover and richness increased, unconstrained by initial conditions. This short-term response suggests that further recruitment and growth are possible, even where early-seral herbs were dominant. Species within this group typically reach peak development two to five years after burning in older forests, then decline, supplanted by forest

species (Dyrness, 1973; Halpern and Franklin, 1990; Schoonmaker and McKee, 1988). However, this transition to forest-species dominance may be delayed by two characteristics of younger stands: pre-fire dominance by early-seral perennials (e.g., *P. aquilinum*) and low abundance of forest shrubs—a legacy of past disturbance. Gustafsson et al. (2021) reached a similar conclusion working in managed (clearcut) forests subject to wildfire. If fire occurs too soon after logging, incomplete recovery of the dominant dwarf shrub may delay the progression from early-seral to forest-species dominance.

Stark differences in species' response to fire make it difficult to generalize about the post-fire dynamics of early-seral shrubs. *Arctostaphylos columbiana*, an obligate seeder lacking a lignotuber (Adams, 1940; Gratkowski, 1978), was highly sensitive to fire, surviving only in unburned plots. Although fire triggered germination from the seed bank, seedling growth may be limited by competition from *P. aquilinum* or shading from surviving trees—conditions not faced by the original, post-harvest cohort. In contrast, *Rubus parviflorus* responded positively to fire, irrespective of severity. Protected by a system of deeply buried rhizomes, *R. parviflorus* is tolerant of high-severity fire and shows rapid recovery in the open (Gucker, 2012; Haeussler and Coates, 1986; Kauffman and Martin, 1990; Stickney, 1981). Although it can colonize disturbed sites via buried or animal-dispersed seed (Kellman, 1970; Morgan and Neuenschwander, 1988; Stewart, 1978), the rapid doubling of cover on our site suggests vegetative regrowth from rhizomes. Unlike *A. columbiana*, *R. parviflorus* is fairly tolerant of shade and is able to persist in the understory for decades at low abundance (Gucker, 2012; Halpern, 1989). Compared to most early-seral shrubs in this region, *A. columbiana* may be an outlier in its sensitivity to fire and dependence on a seed bank. Other common species, e.g., in the genus *Ceanothus*, are facultative sprouters, capable of regenerating from a root-crown or buried seed (Anderson, 2001; Conard et al., 1985; Hickey and Leege, 1970; Johnson, 2000; Lyon, 1971). As a result, where sprouting species such as *Ceanothus* or *R. parviflorus* dominate the shrub layer prior to fire, the response to fire may differ.

Forest generalists showed predictable declines in cover and richness with fire severity, consistent with previous studies in older forests (Dyrness, 1973; Halpern and Franklin, 1990; Halpern and Spies, 1995). Still, we observed considerable variation among and within growth forms (subshrubs vs. herbs and shrubs), consistent with the type and depth of species' perennating structures (Antos and Halpern, 1997; Chapman and Crow, 1981; Flinn and Pringle, 1983; Flinn and Wein, 1988; Schimmel and Granstrom, 1996). Although top-kill reduced the cover of all shrub species, rates of survival and post-fire regeneration varied markedly. Survival was high (>90%) for *Gaultheria shallon* and *Mahonia nervosa*, which resprout from buried rhizomes or stem bases (Tirmenstein, 1990). Both tolerate burning although recovery can be slow after high-severity fire (Haeussler and Coates, 1986; Halpern, 1988, 1989; Lafferty, 1972; Sabhasri, 1961; Tirmenstein, 1990). In contrast, survival was considerably lower (~55%) for *Rhododendron macrophyllum*, whose shallow root crown leaves it susceptible to ground fire (Crane, 1990; Dyrness, 1973; Steen, 1965).

Among herbaceous or semi-woody forest species, those with exposed perennating structures such as stolons (*Viola sempervirens* and *Whipplea modesta*) or a shallow caudex (*Hieracium albiflorum*) declined with fire severity. In contrast, species with tubers, rhizomes, or a taproot (e.g., *Trientalis borealis* ssp. *latifolia* and *Rubus ursinus*), did not. This variation is consistent with past studies relating species' resistance to fire to the relative exposure of their perennating structures (Chapman and Crow, 1981; Pidgeon and Mallik, 2013; Pyke et al., 2010). Despite variation in their sensitivity to fire, few herbs or subshrubs showed marked changes in frequency of occurrence or average cover across the site. This counterintuitive result highlights an important life-history tradeoff in

systems in which burning is spatially patchy: regenerative traits, such as stolons, that leave species susceptible to ground fire, promote growth or expansion in unburned microsites if resource conditions improve (e.g., with loss of tree cover). Many of these species responded similarly to burning in older forests—declining in areas of high-severity fire but expanding in plots that escaped fire (Dyrness, 1973; Halpern, 1989).

4.3. Caveats and limitations

Given few comparable studies of fire in young stands, care must be taken in extrapolating from our results. Both the pre-fire vegetation and pattern of burning were patchy, leaving some plots unburned (with or without trees) and others with complete mortality of the overstory. Fire behavior and vegetation responses to fire may differ in more intensively managed stands or in other biophysical settings. For example, denser plantations with greater continuity of live fuels should experience more uniform and severe fire than our naturally regenerating stand (Kobziar et al., 2009; Odion et al., 2004; Stephens and Moghaddas, 2005; Thompson et al., 2007). Pre-fire suppression of the understory in these more intensively managed plantations may also limit the post-fire contributions of forest species. Conversely, more open, herb-dominated understories with little woody biomass may be more resilient to fire than our shrub-dominated type.

As a case study of a small, albeit intensively sampled site, our work is limited in its spatial scope. Despite use of conventional plant groupings to facilitate comparisons with other systems, our species pool was small and functional-group responses tended to be driven by a few, dominant species. As a result, contrasting responses to fire in some species-poor groups (early-seral shrubs) made it difficult to generalize to the broader regional flora.

Our work is also limited in its temporal scope—to the initial effects of fire. Further sampling is needed to assess the longevity of these short-term effects and to detect any lagged responses to fire. Still, where relatively long-lived perennials dominate the flora and the window for post-fire recruitment is short, initial responses to fire can be indicative of longer-term trends (Noble and Slatyer, 1980). Indeed, in older forests, legacies of high-severity fire can persist for decades after burning (Bowd et al., 2021; Halpern, 1989; Halpern and Spies, 1995; Gustafsson et al., 2021).

5. Conclusions

We examined how pre-fire conditions and fire severity interact to shape community, functional-group, and species' responses to disturbance in a young, naturally regenerating forest in western Oregon. Our results provide a novel perspective on how responses to fire compare to those in older forests, for which there is a richer history of study. At both ends of the sere, pre-fire conditions and fire severity are strong predictors of understory response. However, distinct differences in pre-fire conditions and disturbance history lead to different outcomes in young vs. old forests. First, pre-closure forests are dominated by early-seral perennials with regenerative traits that confer resilience to fire. For example, *Pteridium aquilinum* is a classic endurer (sensu Rowe, 1983) with a well-developed system of rhizomes and renewal buds that ensure survival and rapid regrowth after fire. In contrast, early-seral perennials are uncommon in older forests, thus slower to develop after fire (Halpern, 1989; Halpern and Franklin, 1990; Schoonmaker and McKee, 1988).

Second, legacies of past disturbance in the form of reduced abundance or reproductive potential of forest species, may be exacerbated by short-interval fire (Bowd et al., 2021; Enright et al., 2015; Gustafsson et al., 2021; Johnstone et al., 2016; McCord et al., 2019). The

progressive decline of *Rhododendron macrophyllum* in our site is illustrative: high values of pre-harvest frequency and cover (69 and 48%) remained depressed nearly 30 years later (21 and 8%) and were further reduced by the 2018 fire (12 and 4%). This decline raises the question of whether shortened-interval fire simply resets succession or fundamentally alters the trajectory of understory development, e.g., shifting dominance from fire-sensitive woody species to more fire-resistant or shorter-lived herbaceous species. Johnstone et al. (2016) described similar effects of recurrent disturbance that reduce the resilience of 'material legacies' (e.g., survivors or seeds) leading to novel, post-disturbance outcomes. Similarly, Enright et al. (2015) framed this as one of several possible outcomes of 'interval squeeze', whereby key demographic or vital rates (e.g., seed production or accumulation) fall out of sync with changing climatic and fire regimes. Whether reliance on vegetative propagation leads to similar patterns of species decline—the short-term effects of recurrent fire in this system are clear, favoring early-seral herbaceous perennials over shade-tolerant forest shrubs.

Our study revealed a third, surprising difference in post-fire dynamics of younger vs. older forests. Despite a sizable species pool, annuals contributed minimally to the post-fire vegetation in our young forest. Common wind-dispersed annuals (*Senecio sylvaticus* and *Epilobium brachycarpum*) that establish at high density after burning of older forests, were notably rare. Broader-scale surveys are needed to confirm the generality of this result and to elucidate the underlying causes. Our work suggests that two characteristics of young stands may be key: lower fuel loadings result in less severe fire and less exposure of mineral soil, and the space and resources freed by fire are readily preempted by established early-seral perennials.

As changes in climate and land use alter the frequency, size, and distribution of fires, it becomes increasingly important to understand the context-dependence of fire effects. Our work contributes to a small, but growing literature on plant functional-group responses to fire during the early stages of stand development, when forest understories are still recovering from disturbance. As with older forests, initial characteristics of the vegetation shape responses to fire severity through the regenerative traits of the available species. However, in the short term, distinct differences in the functional composition of young and old stands can lead to very different post-fire outcomes.

CRediT authorship contribution statement

Charles B. Halpern: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Joseph A. Antos:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Funding to establish the original experiment was provided by the USDA National Research Initiative Competitive Grants Program (grant number 91-37101-6895). Cheryl Friesen (Willamette National Forest) provided logistical support. We thank Allison Rossman, Rob Pabst, Scott Abella, and an anonymous review for critiques of earlier drafts of the manuscript.

Appendix A

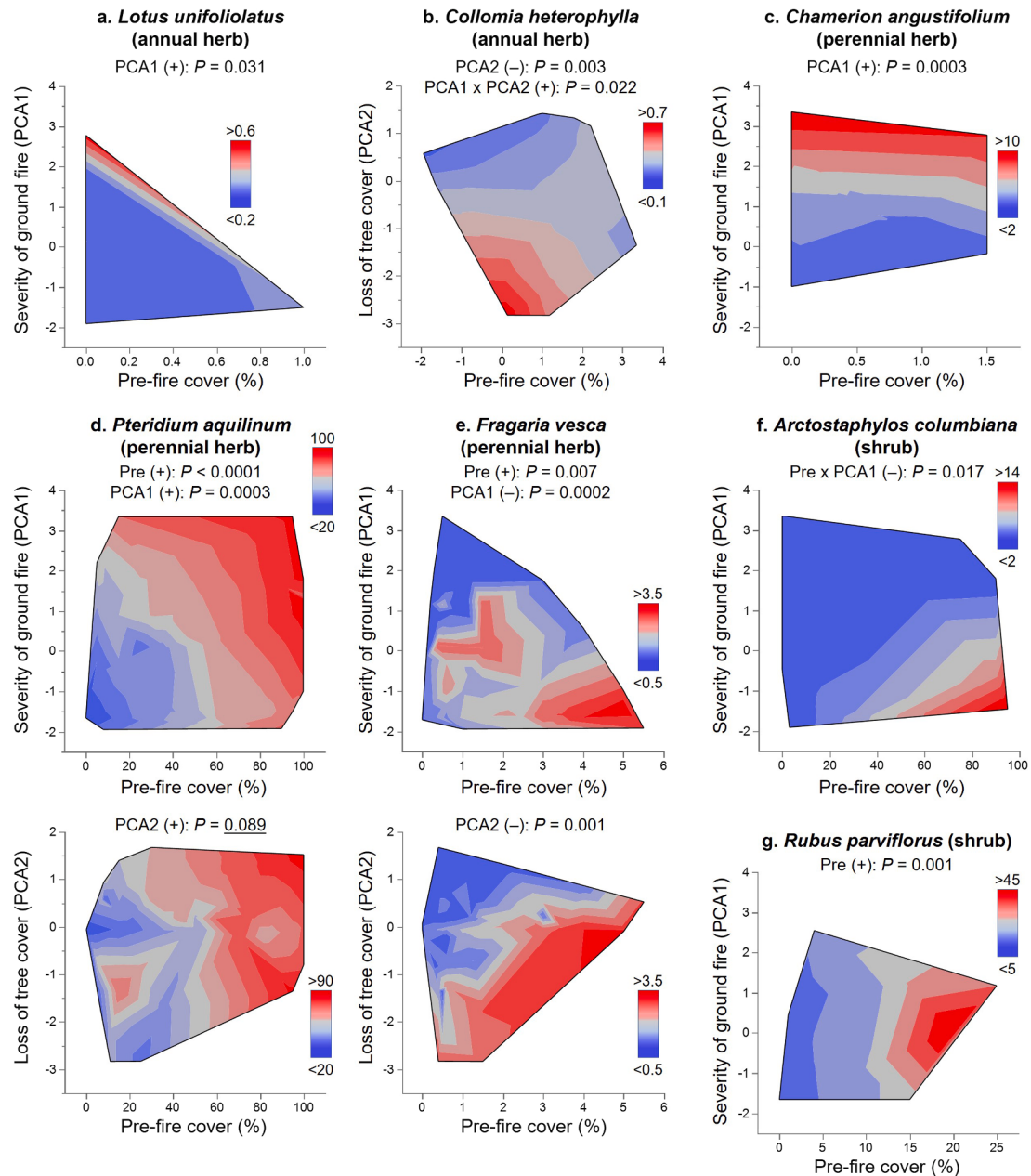


Fig. A1. Post-fire cover of key early-seral species as a function of pre-fire cover, severity of ground fire (PCA1), and loss of tree cover (PCA2). (a, b) Annual herbs, (c-e) perennial herbs, and (f, g) shrubs. Marginal significance ($0.05 < P \leq 0.10$) is noted by an underscore. Table 4 contains full model results. For other details see Fig. 4.

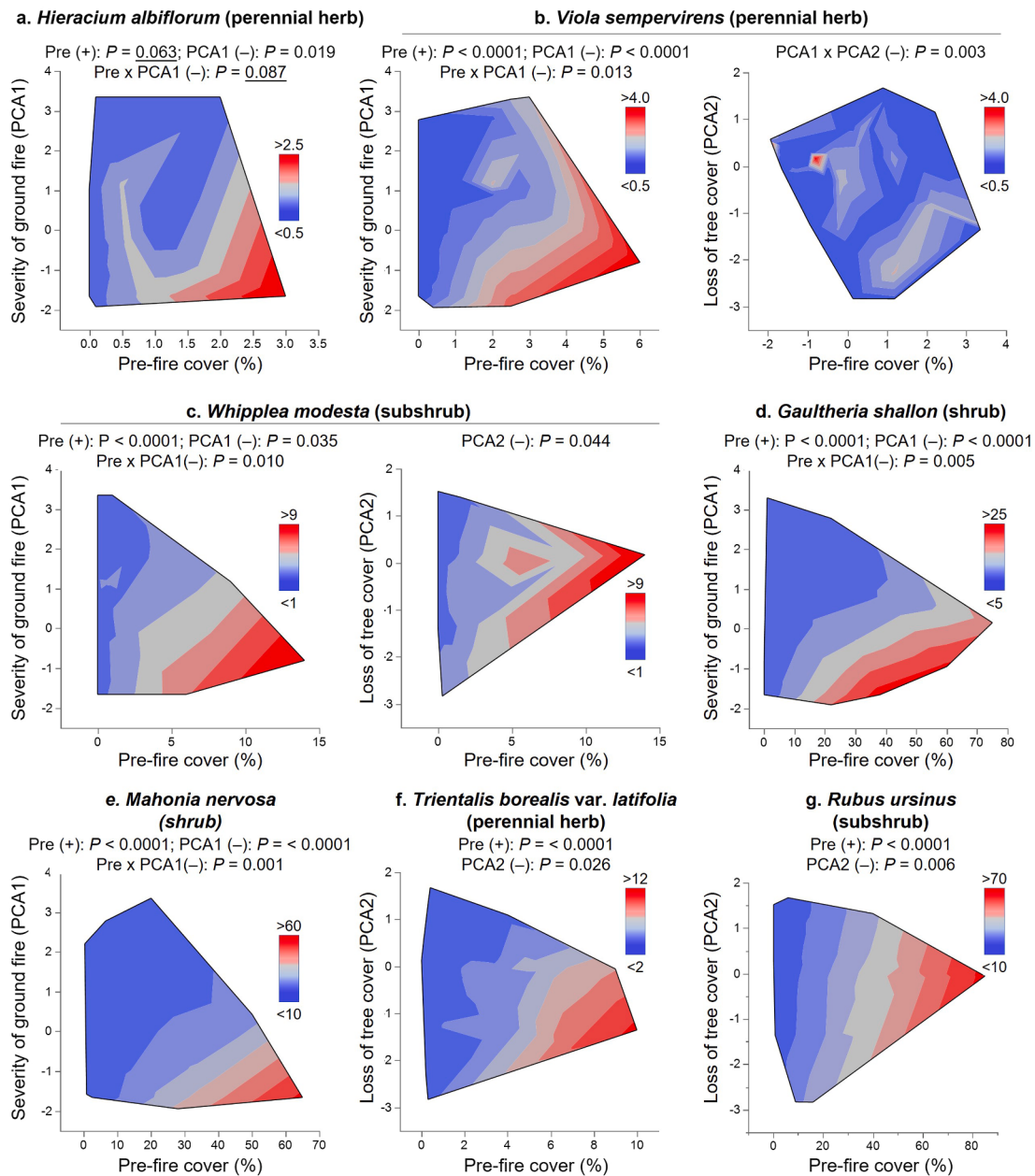


Fig. A2. Post-fire cover of key forest species as a function of pre-fire cover, severity of ground fire (PCA1), and loss of tree cover (PCA2). (a–e) Species responding negatively to fire severity. (f, g) Species unaffected by fire severity but responding positively to loss of tree cover. Marginal significance ($0.05 < P \leq 0.10$) is noted by an underscore. Table 4 contains full model results. For other details see Fig. 4.

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