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Broadcast burning has persistent, but subtle, effects on understory composition and structure: Results of a long-term study in western Cascade forests

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ABSTRACT

Approaches to forest management have changed markedly in the Pacific Northwest in recent decades, yet legacies of past management persist on the landscape. Following clearcut logging, woody residues were typically burned to reduce future fire hazard, create planting spots, facilitate natural recruitment, and retard growth of competing vegetation. We asked whether legacies of broadcast burning persist in the forest understory during the early stages of stand closure, how they manifest structurally or compositionally, whether they are altered by subsequent management (pre-commercial thinning), and how they vary with gradients in the physical environment or stand structure. We used data from 44 pairs of burned and unburned plots sampled 37–42 years after clearcut logging of mature and old-growth forests in western Oregon and Washington. Burning had persistent, but mostly subtle effects on community structure and composition. Burned plots had greater cover of early-seral species and lower cover of woody forest species. Among the latter, tall shrubs showed consistently negative responses to burning. Smaller-statured woody and herbaceous species were more variable in their responses, reflecting a greater diversity of regenerative traits. For some understory attributes, effects of burning were contingent on thinning history. For example, burning enhanced species richness and reduced species evenness, but only in unthinned sites. Conversely, burning increased the spatial variability of tall shrub cover, but only in thinned sites. In some instances, thinning compounded the effects of burning, resulting in a four-fold increase in cover of early-seral herbs and a 50% reduction in cover of forest tall shrubs relative to plots that received neither treatment. For most understory attributes, regional variation in the magnitude of the burn effect was not easily explained by burn severity, site environment, or stand structure. Collectively, our results highlight the persistent, but highly variable, effects of broadcast burning on the post-harvest development of the forest understory. They suggest that, where it is feasible, controlled burning can be used in regeneration-harvest units to achieve a variety of management objectives, with minimal effect on the forest understory.

1. Introduction

Silvicultural practices in the Pacific Northwestern region of the U.S. have changed markedly in recent decades as scientific and societal concerns have shifted the emphases of forest management from timber extraction to multiple resource values (Kohm and Franklin, 1997; Spies et al., 2019; Swanson and Franklin, 1992). One such practice, broadcast burning of logging residues, has a long history of use and debate (Agee, 1989; McCulloch, 1944). During the latter half of the 20th century,

clearcut logging of old and highly productive forests generated large volumes of woody debris (slash), viewed both as a fire hazard and barrier to reforestation. Slash was routinely burned *in situ*, with the goals of reducing fire hazard, facilitating natural recruitment of tree seedlings, creating space for planting, and retarding growth of competing vegetation (Feller, 1982; Morris, 1958). The effects of broadcast burning have been studied from a variety of perspectives, including its efficacy in limiting future spread of fire (Morris, 1970; Munger and Matthews, 1941); impacts on air and water quality (Brown et al., 1973; Fritschen

et al., 1970; Harr and Fredriksen, 1988); loss of soil carbon, nutrients, and site productivity (Antos et al., 2003; Feller, 1982; Kraemer and Hermann, 1979; Miller et al., 1990); and effects on both tree regeneration (Piatek et al., 2003; Vyse and Muraro, 1973) and understory vegetation (Halpern and Franklin, 1990; Morris, 1970; Schoonmaker and McKee, 1988). Syntheses of the literature highlight the difficulty of generalizing across systems because responses to burning are influenced by myriad factors, including fuel and fire characteristics, climate, soils, and the regenerative traits of resident species (Abella and Springer, 2015; Feller, 1982; Neary et al., 1999). Responses to fire can also be time dependent (Rossman et al., 2018; Webster and Halpern, 2010), although few studies are of sufficient duration to capture the time-course of fire effects (Abella and Springer, 2015; Willms et al., 2017).

We address these challenges in the current study, which explores the long-term consequences of broadcast burning for understory vegetation in clearcut forests of western Oregon and Washington, USA. Our analyses are based on a 40-year remeasurement of a regional system of permanent plots established by William G. Morris in the 1940s. The original goals of the study were to test the effectiveness of slash burning for reducing fire hazard, enhancing seedbed and planting conditions, and reducing competition from shrubs (Morris, 1958, 1970). Paired burned and unburned plots were distributed across clearcut harvest units from southern Oregon to southern Washington to establish a broad scope of inference. Early assessments by Morris (1958, 1970) confirmed that broadcast burning could reduce future fire hazard (rate of spread and resistance to control) for as many as 15 years. Over the same period, however, burning did not have a consistent effect on conifer regeneration or competing vegetation (Morris, 1970). For example, during the first decade, increases in herbaceous cover were greater in burned than in unburned plots in the Coast Range, but not in the Cascade Range. In the second decade, cover declined more consistently. Although burning generally suppressed the cover of residual forest shrubs, it triggered the establishment of the seed-banking shrub, *Ceanothus velutinus*, but mainly in the southern Cascades (Kraemer, 1977; Morris, 1970). In the current study, we undertake a more comprehensive and nuanced analysis of the response to burning, extending the time frame to four decades after harvest. By this point, many sites had been pre-commercially thinned to enhance the growth of crop trees, potentially altering responses to burning. Within this broader context, we assess whether legacies of burning persist through stand closure; how they manifest structurally or compositionally; whether they are altered by post-harvest management; and how they vary regionally.

Broadcast burning of logging slash can affect multiple aspects of community structure: promoting recruitment of disturbance-dependent annuals and perennials (Halpern, 1989; Kellman, 1974; Schoonmaker and McKee, 1988); reducing or eliminating forest species that are sensitive to, or slow to recover from, fire (Halpern, 1989; McLean, 1969; Rowe, 1983); and altering the diversity and dominance structure of the vegetation (Halpern and Spies, 1995; Schoonmaker and McKee, 1988; Shafi and Yarranton, 1973a). The characteristic patchiness of post-logging residues can also affect the severity of burning and with it, spatial variation in plant survival and growth (Shafi and Yarranton, 1973b). This heterogeneity can have broader implications for stand development, biodiversity, and other ecological functions (Christensen, 1997; Donato et al., 2012; Fuhlendorf et al., 2006; Wiens, 1997).

The time-course of burn effects can vary widely for different components of the understory. For example, in western coniferous forests, broadcast burning triggers only a brief period of dominance by colonizing annuals and perennials, as microsites for recruitment become increasingly scarce (Compagnoni and Halpern, 2009; Halpern, 1989; Yerkes, 1958). Similarly, post-fire declines may be short-lived for forest herbs that perennate from well-developed systems of roots or rhizomes. In contrast, effects of burning can be more persistent for woody species whose perennating structures are exposed to fire (Halpern, 1989; Halpern and Antos, 2022; Kayes et al., 2010).

Species' responses to burning are shaped by their life-history,

morphological, and regenerative traits (Halpern, 1989; Pyke et al., 2010; Rowe, 1983) and how these traits interact with the characteristics of fire (e.g., burn severity). For example, even moderate-severity fire can eliminate shallow-rooted forest herbs and sub-shrubs whose perennating structures lie in or just below the litter layer (Flinn and Pringle, 1983; Ingersoll and Wilson, 1990; McLean, 1969). In contrast, herbaceous or woody species with deeply buried root systems can survive even intense burning (Antos and Halpern, 1997; Chapman and Crow, 1981; Flinn and Pringle, 1983; Flinn and Wein, 1977). Species' regenerative traits can also dictate their longer-term responses to fire. For example, recovery can be rapid in stoloniferous or rhizomatous forest herbs that can capitalize on sudden increases in light or soil resources ('release' herbs; Halpern, 1989; Lindh and Muir, 2004). In contrast, for species that are eliminated by fire or require more shaded conditions, recovery may hinge on the pace of overstory development or on long-distance dispersal, which can be slow in many forest herbs (Bierzychudek, 1982; Cain et al., 1998; Ehrlén and Eriksson, 2000).

As the primary drivers of post-harvest succession shift from characteristics of the initiating disturbance (e.g., burn severity; Halpern, 1988) to environmental or biotic controls (e.g., site productivity or canopy shading; Bergeron and Dubue, 1988; Christensen and Peet, 1984; Romme et al., 2016), evidence of burning should diminish. Conditions that slow the pace of overstory development (e.g., seed limitations, droughty soils, or a warming climate) may perpetuate early-seral legacies of burning (e.g., the persistence of fire-dependent woody colonists; Donato et al., 2012). Conditions that lead to more rapid closure of the canopy may erase these legacies, while perpetuating others (e.g., further suppression of fire-sensitive forest species).

Evidence of prior burning may be erased, or amplified, by subsequent management activities, such as pre-commercial thinning. These density-reduction treatments, aimed at enhancing the growth of crop trees, have both direct and indirect effects on the understory: exposing mineral soil and physically damaging plants (Ares et al., 2010; Thomas et al., 1999; Wilson and Puettmann, 2007), while increasing light and soil resource availability (Prévost and Gauthier, 2012; Sprugel et al., 2009; Xinzhong et al., 2018). In the process, thinning can alter or compound prior effects of burning, e.g., by favoring the establishment or release of ruderal species that had benefited from fire (Davis and Puettmann, 2009; Thysell and Carey, 2001), or by damaging fire-sensitive forest species, thus further delaying their recovery.

Here, we use a regional system of 44 permanent plots to explore whether, in what form, and under what conditions, broadcast burning of logging slash has had lasting effects on the structure or composition of the forest understory. We pose the following questions:

1. Can we detect effects of broadcast burning in the structure or composition of the forest understory four decades after harvest? If so, which community attributes are most sensitive to burning, and which species—and traits of species—contribute to these responses?

2. Does pre-commercial thinning, conducted two to three decades after harvest, amplify or temper prior responses of the understory to burning?

3. Do the direction or magnitude of understory burn effects vary with fire severity, site environment (latitude, elevation, or heat load), or patterns of overstory development?

2. Methods

2.1. Study area

The study area encompasses conifer-dominated forests at low to moderate elevations (427–1280 m) on federal forestlands in the western Cascade Range of Oregon and Washington, USA (Fig. 1; Table A1, Appendix A). An additional site lies in the Oregon Coast Range. The climate of the region is maritime, characterized by mild wet winters and warm dry summers (Franklin and Dyrness, 1988). During the period of study, mean annual precipitation ranged from 2591 mm yr^{-1} in the
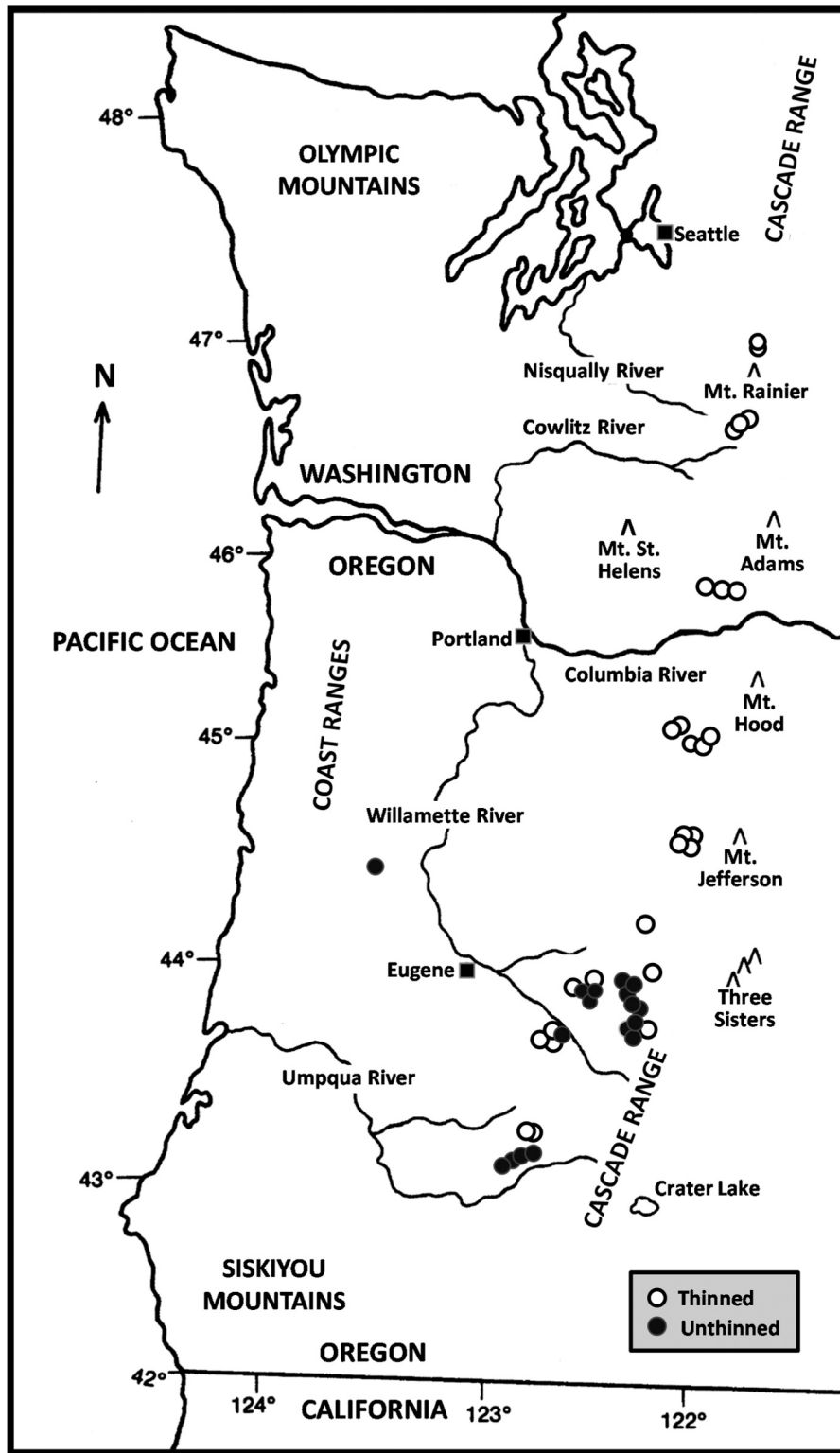
Fig. 1. Locations of the 44 unburned-burned plot pairs in western Oregon and Washington. Thinned and unthinned sites are coded as open and closed symbols, respectively.

north (Wind River, Washington) to 831 mm yr^{-1} in the south (Roseburg, Oregon) (Western Regional Climate Center, https://wrcc.dri.edu/). Average maximum July temperatures ranged from 21.9° C in the north (Rainier Carbon River Station, Washington) to 28.6° C in the south (Roseburg, Oregon).

Study sites represent two forest zones defined by the climax tree species: *Tsuga heterophylla* at lower elevations and *Abies amabilis* at higher elevations (Franklin and Dyrness, 1988; Table A1, Appendix A). At the time they were logged, forests were dominated by 100- to 415-year-old *Pseudotsuga menziesii* with lesser amounts of *Tsuga heterophylla*, *Abies amabilis*, and *A. procera* (Morris, 1970). Historically, forests in this region evolved with episodic fires of varying size and severity,

often separated by long, fire-free intervals (Morrison and Swanson, 1990; Tepley et al., 2013; Weisberg and Swanson, 2003).

Sites encompass a broad range of slopes and aspects (Table A1, Appendix A), typical of these dissected mountain landscapes. Soils are generally deep (>1 m) and well-drained. Most derive from underlying flows of andesite and basalt or pyroclastic tuffs and breccias (Franklin and Dyrness, 1988; Morris, 1970). Deposits of ash of varying age overlie residual soils near the younger volcanic peaks of the High Cascades (Franklin and Dyrness, 1988).

2.2. Study design and field methods

This study was initiated in 1945 by William G. Morris with the goals of comparing future fire hazard, conifer regeneration, and growth of competing vegetation in clearcuts that were subsequently burned or not (Morris, 1958, 1970). Sample plots were established over a 7-year period at 63 sites; 44 of these are included in the current study (Table A1, Appendix A). Harvest units of 12–24 ha were clearcut between 1945 and 1951. Merchantable logs were yarded by cable or tracked skidder, leaving an average of 140 Mg ha^{-1} of logging slash (Miller and Bigley, 1990). At each site, two permanent, rectangular plots (25 × 40 m) were established ~20–80 m apart in areas of comparable slope, aspect, soils, slash loading, shrub cover, and distance to coniferous seed sources (Morris, 1958, 1970). One of the two plots was then broadcast burned. At all but two sites, burning occurred in late summer or fall in the same or subsequent year as logging. Slash consumption averaged ~37% or ~50 Mg ha^{-1} (Miller et al., 1990). Burning consumed nearly all downed branches with fine twigs, but did not appreciably reduce the volume of larger logs (>30 cm in diameter). On average, 60% of the ground surface was lightly burned (forest floor and woody debris only partially consumed); 20% was moderately burned (forest floor and woody debris consumed or deeply charred and color of mineral soil unaltered); and <6% was severely burned (color of the upper mineral horizon altered and often reddish) (Morris, 1958, 1970). Cover of mineral soil averaged 50% on burned plots and 22% on unburned plots (Morris, 1958, 1970). Burning also eliminated most advance regeneration (Miller et al., 1990).

Plots were remeasured multiple times after harvest (Kraemer, 1977; Morris, 1958; 1970; Steen, 1966), but methods and intensity of sampling varied, precluding a meaningful assessment of temporal trends for the current analysis. In 1986 and 1987, 44 sites were identified for remeasurement after a review of site conditions and historical documents confirmed that plot pairs had comparable physiography, soils, and histories of post-harvest management (Table A1, Appendix A). Of the 44 sites, 15 had been planted at unknown density with 2- to 3-year-old seedlings of *Pseudotsuga menziesii* or *Pinus ponderosa* (but survival was poor in six of these). Fourteen sites were fertilized with nitrogen. Twenty-seven sites were pre-commercially thinned 14–37 years after harvest (mean of 26 years). Because thinning was not applied as an experimental treatment, it is possible that thinned sites had naturally greater stand densities than unthinned sites. Thinned and unthinned sites also differed in their geographic and elevational distributions. Thinned sites encompassed the full range of latitudes but unthinned sites were limited to southern and central Oregon (Fig. 1). Thinned sites also occurred at somewhat lower elevations than unthinned sites (means of 828 vs. 998 m). Given these caveats, we approach the interpretation of thinning effects with caution. We do not address effects of planting or fertilization due to the unbalanced or transient nature of those treatments. Additional details on site characteristics and management history can be found in Miller et al. (1990).

Sampling was conducted between June and October in 1986 or 1987, 37–42 years after harvest (mean of 38 years). For pre-commercially thinned sites, sampling occurred 2–22 years after thinning (mean of 11.5 years). In each plot, all live trees (hardwoods and conifers ≥4.1 cm diameter at breast height or dbh) were identified to species and measured for diameter (nearest cm). Heights (nearest dm) were

estimated for 25 of the canopy dominants. Canopy cover (including conifers and hardwoods) was estimated by cover class (<5%, 5 to <25%, 25 to <50%, 50 to <75%, 75 to <95%, and 95–100%) above each of 15 understory subplots. Subplots were 2.3 m in radius (~16.6 m^2 in area) and spaced ~8 m apart in a 3 × 5 array within each plot. Additional details on overstory sampling can be found in Miller et al. (1990).

Cover of each understory species (including hardwoods <4.1 cm dbh) was also estimated by cover class in each of the 15 subplots. Several taxa could not be consistently identified to species and were treated at the genus or family level (Table A2, Appendix A). Plant nomenclature follows the USDA Plants Database (USDA and NRCS, 2021).

2.3. Data manipulation

2.3.1. Species' classification by seral role and growth form

Our core analyses focus on groups of understory species defined by their seral roles and growth forms (Table A2, Appendix A). Group assignments follow those used in prior studies of forest understory development (Halpern, 1989; Halpern and Spies, 1995; Halpern et al., 2012; Thomas et al., 1999). Seral roles were defined very broadly as 'early seral' and 'forest', to distinguish species of disturbed, open habitats from those of closed-canopy forests. The latter include 'release' species (which respond positively to overstory removal in the short term); successional generalists (present at all stages of forest development); and late-seral or old-growth associated species, which were uncommon in this study (Halpern, 1989; Halpern and Spies, 1995; Lindh and Muir, 2004; McKenzie et al., 2000). Several taxa that could not be classified by seral role were excluded from seral-group analyses; most contributed minimally to the vegetation (Table A2, Appendix A).

We distinguished five growth forms, defined by the presence/absence of woody perennating structures and, among woody groups, by height at maturity. These included herbs (forbs, ferns, and graminoids) and four woody growth forms of increasing stature, with progressively greater allocation to stem mass: sub-shrubs, low shrubs, tall shrubs, and understory hardwoods.

2.3.2. Univariate measures of understory response

We estimated the abundance of each species as the mid-point of its cover class. For each subplot, species' cover values were summed to generate totals for each seral group and growth form within each group (early-seral species included only herbs, tall shrubs, and hardwoods; Table A2, Appendix A). Subplot values were then used to compute plot means and to characterize the variation (or spatial heterogeneity) in plant cover and species composition within plots. Variation in cover was expressed as the coefficient of variation (CV) of subplot values for each of two height-based understory layers: the herb layer (summed cover of herbs, sub-shrubs, and low shrubs) and the tall-shrub layer. We did not consider the variability in cover of hardwoods due to their sparse distributions and low cover. Heterogeneity in composition was expressed as the mean Bray-Curtis dissimilarity of subplots, computed from a matrix of arcsine square-root transformed species-cover data.

Using the Hill diversity series (Hill, 1973; Magurran, 1988; Roswell et al., 2021), we computed three indices—richness, diversity, and evenness—to characterize the number and distribution of abundance among species. Richness (N_0) was computed at two spatial scales—number of species per plot (243 m^2) and mean number of species per subplot (16.6 m^2)—for each seral group and for species in total. Trends were similar between scales, thus we limit our presentation to plot richness. Species diversity, which considers both the number and relative abundance of species, was computed at the plot scale as Hill's N_1, the exponential of Shannon's index (Hill, 1973; Roswell et al., 2021):

$$N_1 = \exp \Sigma \ (p_i \times \ln p_i)$$

where p_i is the proportional cover of the ith species in the plot. N_1 shares the same units as richness but is less sensitive to the presence of

uncommon species. It is commonly described as the 'number of abundant species' or the 'effective number of species' (Alatalo and Alatalo, 1977; Jost, 2006; Peet, 1974). Species evenness, E (the equitability of species' abundance), was computed at the plot scale using Alatalo's (1981) modification of the Hill ratio of N_2 to N_1:

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

where N_2 is the reciprocal of Simpson's index $(1/\Sigma p_i^2)$. Evenness can be viewed as the ratio of 'very abundant to abundant species' (Alatalo, 1981). Values range from 0 to 1.

2.3.3. Measures of overstory structure and composition

We characterized the overstory composition and structure of each plot to aid in the interpretation of understory responses to burning and thinning (see Section 2.4.1). Tree-based measurements were used to compute the density and basal area of each species and several aggregate measures of overstory structure: total density and basal area, density of conifers and hardwoods, and stand density index (SDI, calculated as $\sqrt{[\text{total density} \times \text{total basal area}]}$). We also computed the mean tree height (from the 25 dominants in each plot), and mean canopy cover (from the 15 subplot estimates of cover).

2.4. Statistical analyses

2.4.1. Univariate measures of response

We used a series of mixed-effects, split-plot ANOVA models to test responses to burning (question 1) and whether thinning altered these responses (question 2). Fixed effects included burn treatment (UB vs. B, the 'subplot' factor), thin treatment (UT vs. T, the 'whole plot' factor), and the burn × thin interaction. Site was treated as a random effect. Significant burn × thin interactions were followed by post-hoc *t*-tests of model-estimated marginal means to assess the significance of burning in each thinning context.

Because understory responses to treatments can be shaped indirectly through effects on overstory development, we first tested the effects of burning and thinning on overstory structure. Models were run on the density and basal area of the primary tree species and on the aggregate measures of structure (see Section 2.3.3). We then tested understory responses to treatments. Models were run for (1) cover of seral groups and growth forms within each group, (2) cover of the most common species within each growth form × seral group, (3) indices and components of diversity, and (4) measures of within-plot variation in cover and composition. Species' models were used to interpret seral-group and growth-form responses—namely, whether responses were generalizable or driven by the dominant species in each group. Species' models were limited to taxa present in ≥25% of the sites, as well as *Ceanothus velutinus* (which had been prominent on burned plots in the past; Kraemer, 1977; Morris, 1970). Sample sizes for these models varied because sites were excluded if a species was absent from both plots. For all models, we tested for homogeneity of variance in the response data and for normality of model residuals. When necessary, data were square-root, log, or arcsine square-root transformed (using the latter for species' cover). Although there were instances in which model assumptions could not be met, raw and transformed data yielded qualitatively similar results.

We ran an additional set of mixed-effects models on thinned sites (*n* = 27) to determine whether responses to treatments varied with time since thinning (range of 2–22 years). This approach assumes that sites shared comparable physical environments and vegetation prior to thinning—a questionable assumption given the geographic dispersion of sites (Fig. 1; Table A1, Appendix A). Response variables included the aggregate measures of overstory structure and all understory metrics (excluding species' cover). Fixed effects included time since thinning, burn treatment (nested within site), and the time × burn interaction; site was treated as a random effect. Where diagnostic tests dictated, response

data were square-root or log transformed. If 'time' or the 'time × burn' interaction was significant, we report results in conjunction with those of the corresponding full-treatment (all-sites) models.

2.4.2. Multivariate (compositional) measures of understory response

We used several approaches to examine compositional responses of the understory to burning and thinning (questions 1 and 2). First, we conducted a non-metric multidimensional scaling (NMS) ordination of the plot × species cover matrix. Prior to analysis, rare taxa (present at <5% of sites) were removed and cover was arcsine square-root transformed. The analysis was run with PC-ORD ver. 7.10 (McCune and Mefford, 2018) using the 'slow and thorough' autopilot setting, Bray-Curtis as the dissimilarity measure, a random start, a maximum of 500 iterations (250 runs each of real and randomized data), and an instability criterion of 1×10^{-7} (McCune and Grace, 2002). A scree plot of stress vs. number of dimensions (axes) was used to select the final dimensionality (McCune and Grace, 2002). The ordination was displayed as a series of bi-plots with sample plots coded by burn treatment, thinning history, and forest zone; and with a vector overlay showing relationships between ordination axes and environmental or structural variables. To aid in the interpretation of the NMS, we used a series of box plots to compare the distributions of dissimilarity within burn treatments (UB or B) to those of the plot pairs (UB–B), or subsets of plot pairs grouped by thinning history or forest zone. Two-sample *t*-tests were used to determine whether the dissimilarity of plot pairs differed for thinning histories or forest zones. Three sites classified as transitional (*Tsuga-Abies*; Table A1, Appendix A) were excluded from the zonal comparisons.

To supplement the NMS, we performed a series of multi-response permutation procedures (MRPP; McCune and Grace, 2002; Mielke and Berry, 2001) testing whether, and in which contexts, species composition differed between burn treatments. This non-parametric procedure compares the weighted average distance of plots within groups ($\delta_{observed}$) to an expected average distance ($\delta_{expected}$) approximated from the mean distance of all possible partitions of the data of equivalent size. MRPP produces a test statistic, *T*, ($\delta_{observed} - \delta_{expected}$)/standard deviation of $\delta_{expected}$; a *P* value expressing the likelihood of obtaining a δ as or more extreme than the $\delta_{observed}$ given the distribution of possible δs; and an effect size, *A*, termed the chance-corrected within-group agreement (McCune and Grace, 2002). We used MRBP, a blocked variant of MRPP, to account for the pairing of plots at each site. Separate analyses were run for the full set of sites and for sites representing each thinning history and forest zone. Prior to each analysis, we removed rarer species: those present in <5% of sites or, for the *Abies* zone which had only nine sites, <10% of sites. Analyses were implemented in PC-ORD ver. 7.10 using the default settings (McCune and Mefford, 2018).

2.4.3. Relationships with burn severity, physical environment, and overstory structure

We used stepwise linear regression to explore whether variation in the magnitude of the burn effect was related to burn severity, site environment, or patterns of overstory development (question 3). From the larger set of response variables, we chose six: total cover of early-seral and forest species, and cover of the primary forest growth forms—herbs, sub-shrubs, low shrubs, and tall shrubs. For each variable at each site, a burn effect was computed as the difference in cover between burn treatments (B minus UB, with positive values equating to greater cover in B). From the set of potential predictors we chose seven: burn severity, three measures of site environment, and three measures of the difference in overstory development between B and UB plots. Burn severity was expressed as the percentage of ground surface rated as moderately or severely burned (range of 0–100%; see Section 2.2; Morris, 1970). Measures of site environment included latitude, elevation, and heat load (an index of potential direct incident radiation and temperature derived from slope, aspect, and latitude; McCune and Keon, 2002). We used a Pearson correlation matrix to reduce the number of highly correlated overstory predictors. Three were selected: difference between B and UB in canopy cover, total

density, and total basal area (range of *r* of 0.20–0.51). Regression models were developed in JMP Pro 17.0.0 (SAS, 2022) using forward selection and the minimum Bayesian Information Criterion (BIC) as a basis for choosing the "best" model.

3. Results

3.1. Overstory development

After four decades, overstory structure varied widely among plots. Tree density ranged from 336 to 2531 ha^{-1}, basal area from 3.4 to 40.4 m^2 ha^{-1}, canopy cover from 7 to 89%, and dominant tree height from 7.3 to 26.3 m. Conifers greatly outnumbered hardwoods in nearly

all plots. *Pseudotsuga menziesii* was the primary tree species, accounting for >50% of all stems and >70% of the basal area.

Burning had no effect on most aggregate measures of overstory structure, including total and conifer density, total basal area, SDI, canopy cover, and dominant tree height (Fig. 2a). One exception was hardwood density, which was nearly twice as high in B as in UB, but only in unthinned sites (marginally significant burn × thin interaction; Fig. 2a). Nevertheless, hardwoods accounted for fewer than 10% of stems. In contrast, burning had strong effects on overstory composition (Fig. 2b), enhancing the density and basal area of early-seral *Pseudotsuga* and *Prunus emarginata*, and reducing the density and basal area late-seral *Tsuga heterophylla* and *Abies amabilis* (Fig. 2b).

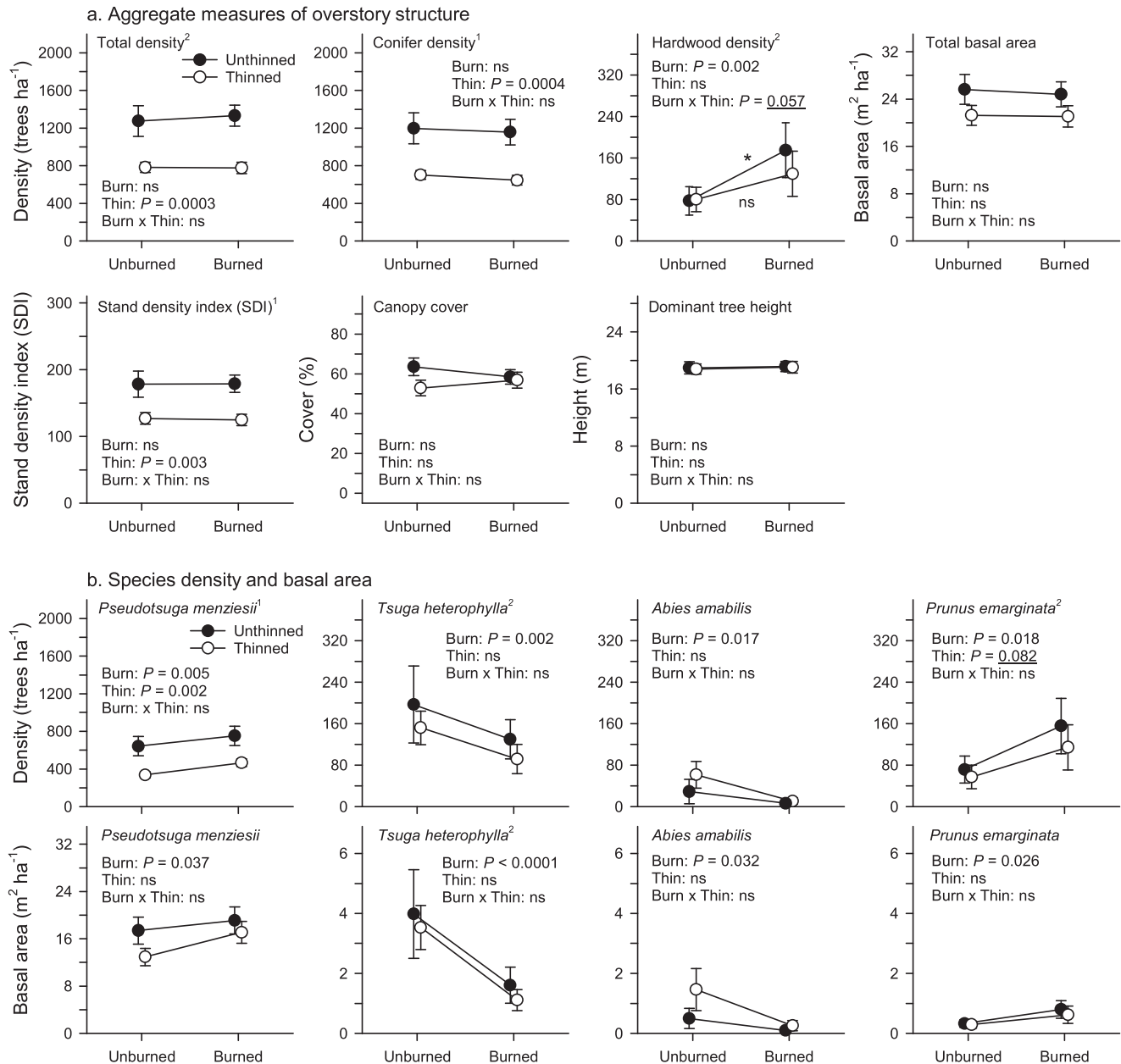At the time of sampling, pre-commercial thinning had reduced total,

Fig. 2. Effects of burning and pre-commercial thinning on (a) aggregate and (b) species-level measures of overstory structure. Means and standard errors (SEs) are based on all sites (*n* = 44; *n* = 43 for canopy cover). Note the variation in scale of the density and basal-area axes. SDI is computed as $\sqrt{\text{(total density} \times \text{total basal area)}}$. Dominant tree height is the mean of 25 dominant stems per plot. Superscripts indicate a [1]square-root or [2]log transformation of the response data. *P* values are shown for significant (*P* ≤ 0.05) main effects and interactions from a mixed-effects, split-plot ANOVA. Marginal significance (0.05 < *P* ≤ 0.1) is indicated by an underscore and non-significance by ns. *P* values are not adjusted for multiple comparisons. For a significant burn × thin interaction, * and 'ns' codes indicate a significant or non-significant burn effect in each thinning context (as determined from post-hoc tests on model-estimated marginal means).

conifer, and *Pseudotsuga* density by an average of ~40%, *Prunus* density by ~25%, and SDI by ~30% (Fig. 2a and b). In contrast, thinning had no effect on total basal area, hardwood density, canopy cover, or tree height (Fig. 2a). Among thinned sites, nearly all measures of structural development were positively correlated with time since thinning; only

hardwood density was not (Table A3, Appendix A).

3.2. Floristics of seral groups and growth forms

We recorded 87 taxa among the 44 sites—a conservative estimate of

Fig. 3. Effects of burning and pre-commercial thinning on the mean cover (±1 SE) of (a) all early-seral species, (b) early-seral herbs, and (c) early-seral tall shrubs, and of the common species within each group (those present in ≥25% of the sites). Seral-group and growth-form values (left column) are based on all sites (*n* = 44); species' values are based on sites in which a species was present (*n* varies). Note the variation in scale of the cover axes. Superscripts indicate a [1]square-root, [2]log, or [3]arcsine square-root transformation of the response data. See Fig. 2 for other details.

total richness given that some taxa were grouped at the genus or family level (Table A2, Appendix A). Nearly all species (84) were native, and the three non-natives were rare (present at fewer than three sites). Annuals were also rare (two taxa, a total of three occurrences). Residual forest species outnumbered early-seral species (54 vs. 22; 11 unclassified), and herbs (46) and tall shrubs (21) outnumbered sub-shrubs (9), low shrubs (5), and hardwoods (6). Except for a small set of uncommon taxa (those with fewer than three occurrences), no species were

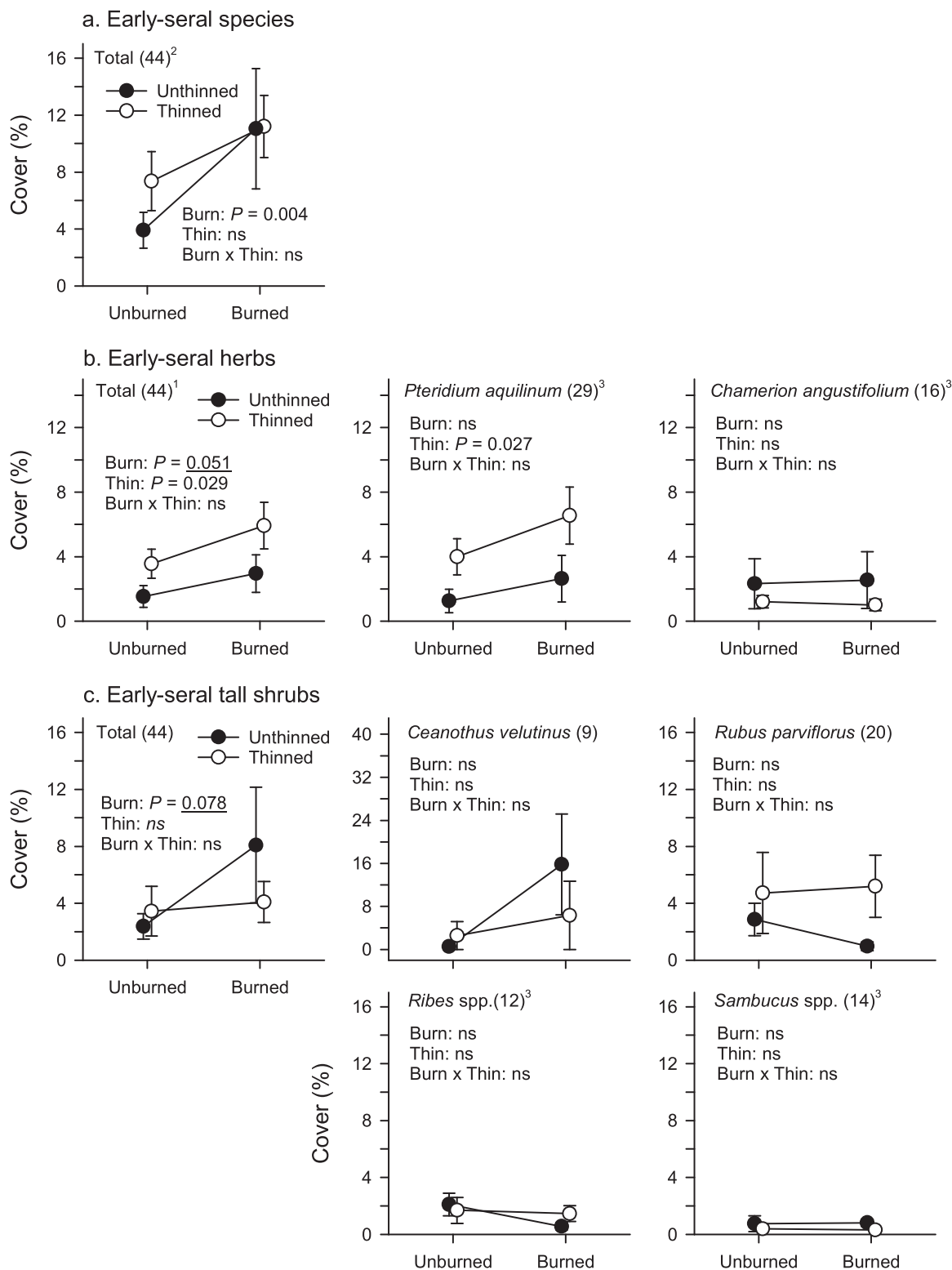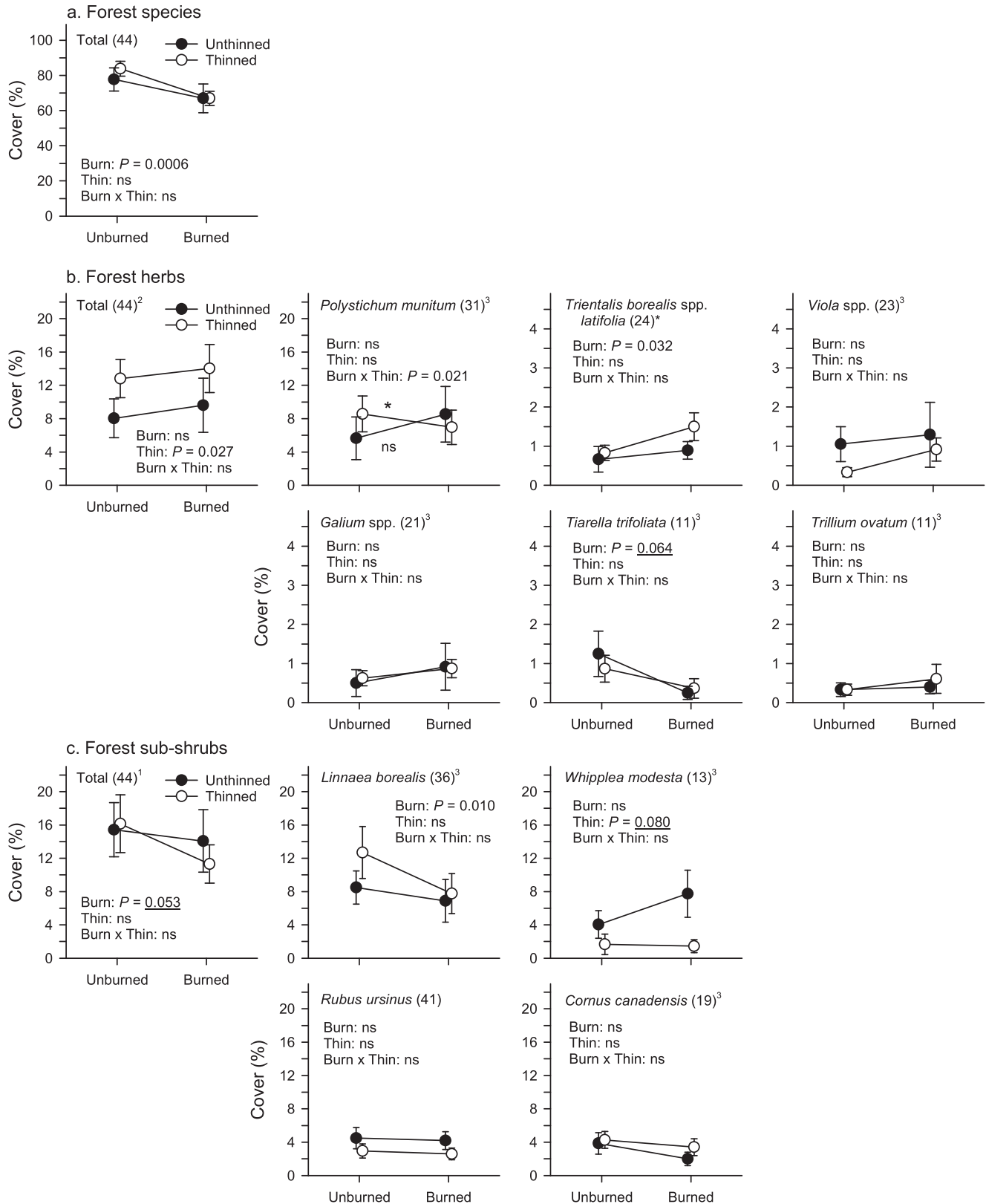**Fig. 4.** Effects of burning and pre-commercial thinning on the mean cover (±1 SE) of (a) all forest species, (b) forest herbs, and (c) forest sub-shrubs, and of the common species within each group (those present in ≥25% of the sites). See Figs. 2 and 3 for other details.

restricted to unburned (UB) or burned (B) plots (Table A2, Appendix A).

3.3. Abundance of seral groups, growth forms, and common species

Four decades after harvest, early-seral species contributed minimally to the vegetation. Nevertheless, their total cover was significantly greater in B than in UB (means of 11.1 vs. 6.0%; Fig. 3a). Except for the clonal fern, *Pteridium aquilinum*, the common taxa occurred at fairly low cover (means of ~0.5–4%) in fewer than half of the sites. Total cover of early-seral herbs and tall shrubs was marginally greater in B than in UB, but cover of the most common taxa within each group was not (Fig. 3b and c). Similar to burning, thinning enhanced the total cover of early-seral herbs (Fig. 3b) and of *Pteridium* in particular. However, thinning did not alter the effect of burning for either early-seral group (non-significant burn × thin interactions; Fig. 3b and c).

Burning had a negative effect on the total cover of forest species (means of 81.2 vs. 66.5% in UB vs. B; Fig. 4a), but it had no effect on the total cover of forest herbs (Fig. 4b). Among herbaceous species, the response to burning varied widely: it was negative in *Tiarella trifoliata*; positive in *Trientalis borealis* ssp. *latifolia* and *Viola* spp.; neutral in *Galium* spp. and *Trillium ovatum*; and contingent on thinning history in *Polystichum munitum* (Fig. 4b). In contrast to burning, thinning enhanced the total cover of forest herbs (Fig. 4b), with greater cover on sites that had been thinned earlier (Table A3, Appendix A). Nevertheless, none of the common species showed significant responses to thinning (Fig. 4b).

Nearly all woody forest growth forms responded negatively to burning (Fig. 4c, Fig. 5). Relative to unburned plots, reductions in cover averaged ~22% in forest sub-shrubs (Fig. 4c), ~16% in forest low
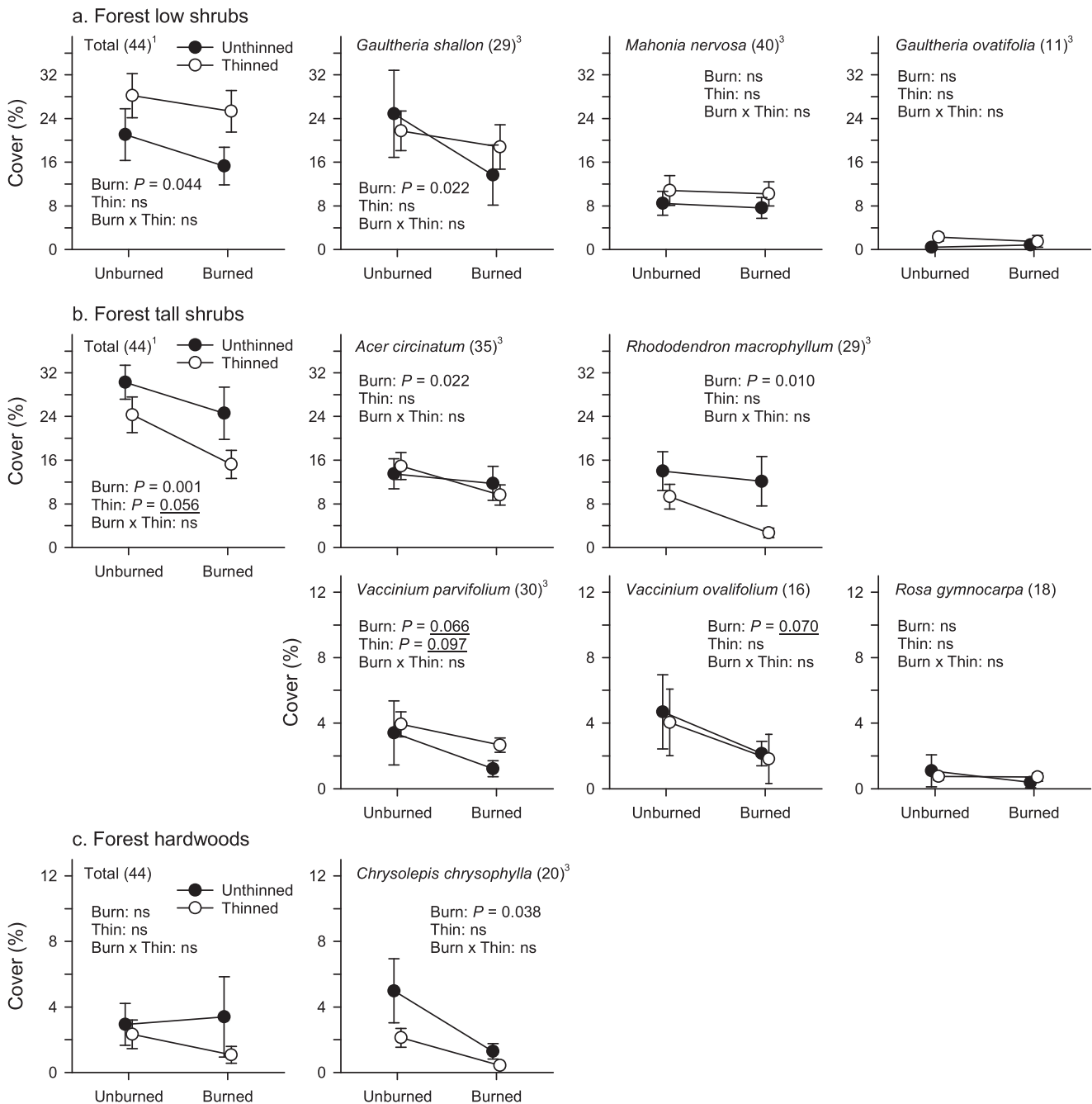

Fig. 5. Effects of burning and pre-commercial thinning on the mean cover (±1 SE) of (a) forest low shrubs, (b) forest tall shrubs, and (c) forest hardwoods, and of the common species within each group (those present in ≥25% of the sites). See Figs. 2 and 3 for other details.

shrubs (Fig. 5a), and ~29% in forest tall shrubs (Fig. 5b). Declines in sub-shrubs and low shrubs were attributable to the dominants, *Linnaea borealis* (Fig. 4c) and *Gaultheria shallon* (Fig. 5a), respectively. All other common species showed neutral responses to burning. In contrast, nearly all tall shrubs responded negatively to burning (Fig. 5b), including dominant (*Acer circinatum* and *Rhododendron macrophyllum*) and subordinate (*Vaccinium parvifolium* and *V. ovalifolium*) taxa. Forest tall shrubs also responded negatively to thinning (Fig. 5b). Total cover was reduced by nearly 40%, with greater losses in sites that were thinned in the more distant past (negative response to time since thinning; Table A3, Appendix A). Much of this decline was attributable to *Rhododendron*, although neither the thin nor burn × thin interaction terms were statistically significant (Fig. 5b).

Forest hardwoods contributed minimally to the understory (mean cover of 2.4%) and their total cover was unaffected by burning or thinning (Fig. 5c). However, the most common species, *Chrysolepis chrysophylla*, showed a marked decline on burned plots (Fig. 5c).

3.4. Measures of diversity and within-plot variation

We recorded an average of 15.1 species per plot, with 4.5 times as many forest as early-seral species (Fig. 6a). Burning enhanced total and early-seral richness in unthinned sites, but not in thinned sites (significant burn × thin interactions; Fig. 6a). In contrast, burning had no effect on the richness of forest species nor on total diversity (Hill's N_1, the number of 'abundant' species; Fig. 6a). Evenness (the equitability of species' abundance) was reduced by burning in unthinned sites, but not in thinned sites (significant burn × thin interaction; Fig. 6a).

Burning had little effect on within-plot variation in plant cover or composition (Fig. 6b), with one exception: burning enhanced the variation in tall shrub cover in thinned sites (but not in unthinned sites; significant burn × thin interaction, Fig. 6b). This variation also increased with time since thinning (Table A3, Appendix A). In contrast to its effect on tall shrubs, thinning reduced variation in cover in the herb layer (sum of herbs, sub-shrubs, and low shrubs; Fig. 6b), and increasingly so with time since thinning (Table A3, Appendix A). Thinning also reduced the compositional heterogeneity of subplots
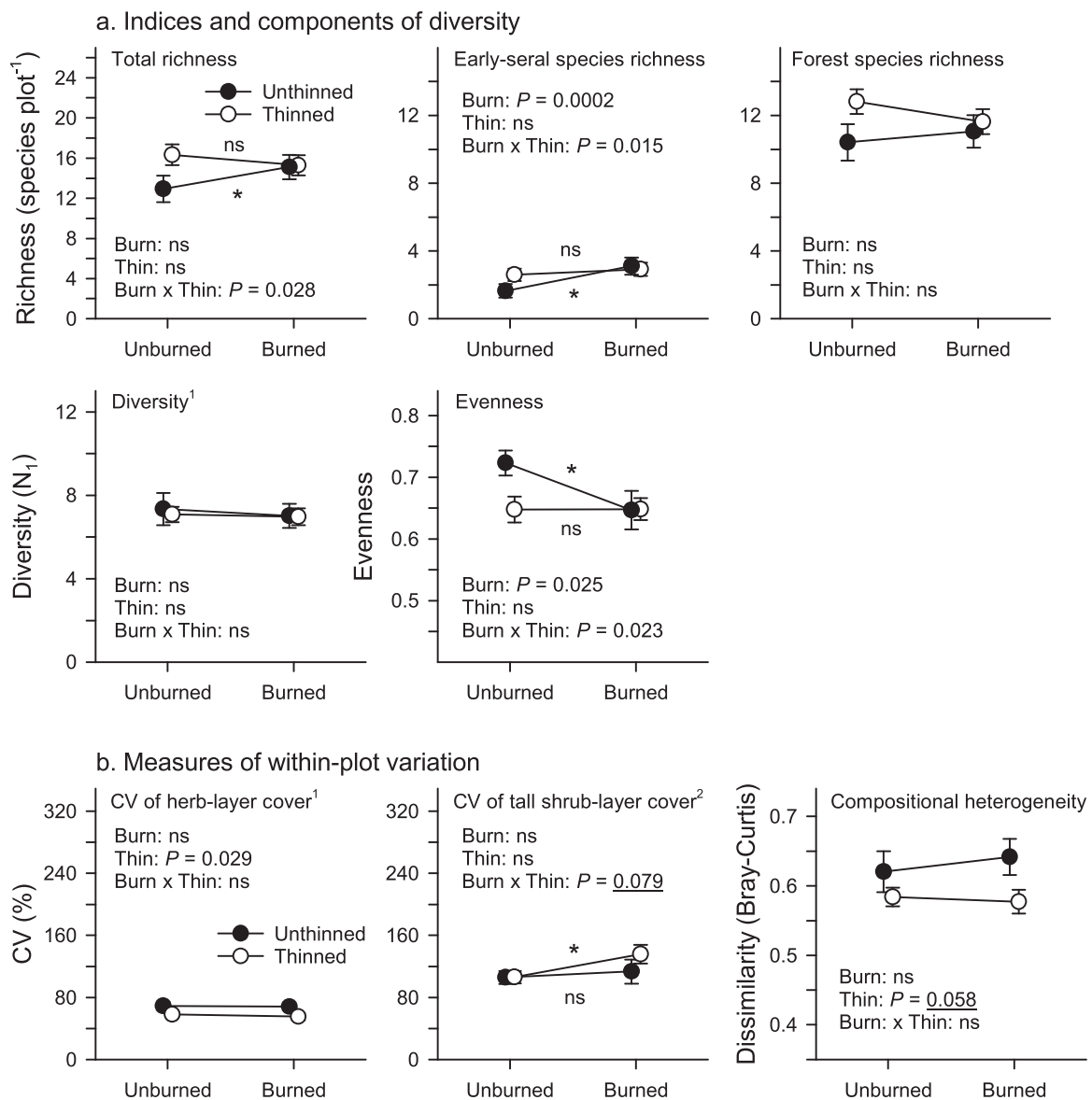

Fig. 6. Effects of burning on (a) indices and components of diversity and (b) measures of within-plot variation. CVs of cover include species from both seral groups. CV of herb-layer cover combines the cover of herbs, sub-shrubs, and low shrubs. Compositional heterogeneity is the mean Bray-Curtis dissimilarity among subplots. See Fig. 2 for other details.

(Fig. 6b).

3.5. Species composition

Based on a scree plot, we selected a final three-dimensional solution for the NMS ordination (stress of 17.2). We focus on the first two dimensions, which showed strong correlations with environmental and overstory structural variables (Fig. 7). Most paired plots (UB and B) were closely associated in ordination space (Fig. 7a), but plots representing

the same burn treatment (UB or B) or thinning history (UT or T) were widely dispersed. Centroids for burn treatments and thinning histories were considerably closer than were centroids for the two major forest zones (Fig. 7a and b). Box-plots summarizing the distributions of inter-plot distances reinforce these patterns: on average, plots representing the same burn treatment (UB or B) were far more dissimilar than were paired plots (Fig. 7c). Paired plots were more similar in thinned (T) than in unthinned (UT) sites (two-sample *t*-test: $t = 2.76$, $P = 0.010$), but comparably similar in the *Tsuga heterophylla* and *Abies amabilis* zones
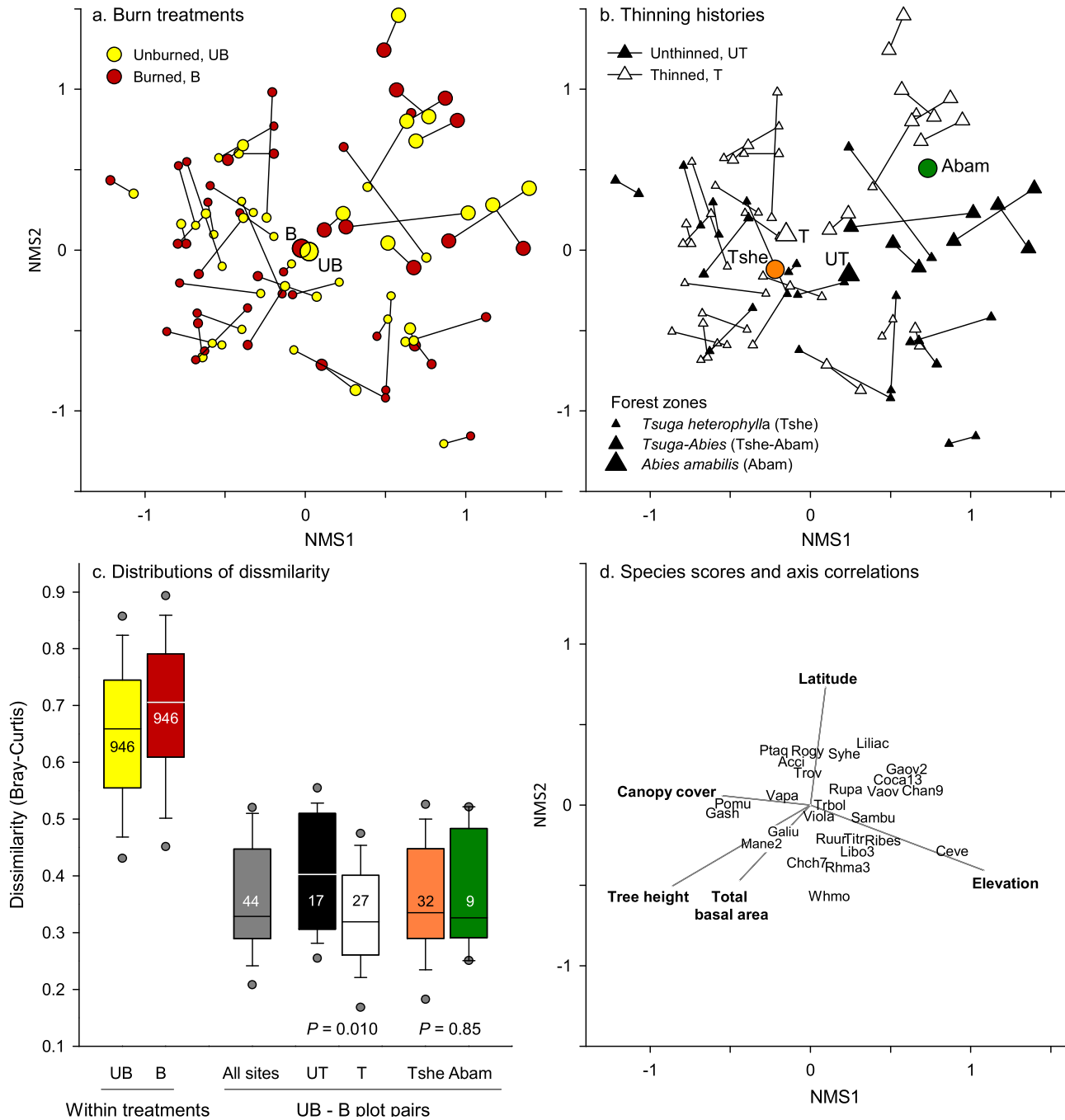
Fig. 7. NMS ordination of plots coded by (a) burn treatment (UB, B) and (b) thinning history (UT, T). Paired plots are joined, forest zones are coded by symbol size, and centroids of burn treatments, thinning histories, and forest zones are large labeled symbols. (c) Distributions of dissimilarity within burn treatments (UB or B) and between UB–B plot pairs (for all sites, UT vs. T, and Tshe vs. Abam zone). Medians are represented by horizontal lines, first and third quartiles by boxes, 10th and 90th percentiles by whiskers, and 5th and 95th percentiles by circles. Sample sizes (number of pairwise comparisons) are noted in each box. *P* values are from *t*-tests comparing the dissimilarity of UB–B plot pairs between thinning histories or forest zones. (d) Species scores for the more common taxa (see Table A2, Appendix A for full names) and axis correlations with environmental and structural variables (grey vectors). NMS1 correlates with elevation (+0.72), dominant tree height (–0.57), and canopy cover (–0.37). NMS2 correlates with latitude (+0.50), dominant tree height (–0.34), and total basal area (–0.31).

(two-sample *t*-test: $t = -0.20$, $P = 0.85$) (Fig. 7c).

Both axes showed strong correlations with site characteristics (Fig. 7d). NMS1 was positively correlated with elevation ($r = 0.72$) and negatively correlated with dominant tree height (–0.57) and canopy cover (–0.37). NMS2 was positively correlated with latitude ($r = 0.50$) and negatively correlated with tree height (–0.34) and total basal area (–0.31). Sites at more northerly latitudes and higher elevations supported species characteristic of the *Abies amabilis* zone (e.g., *Cornus canadensis*, *Gaultheria ovatifolia*, and *Vaccinium ovalifolium*; Fig. 7d). More southerly sites were distinguished by *Ceanothus velutinus* at higher elevations; *Whipplea modesta*, *Rhododendron macrophyllum*, and *Chrysolepis chrysophylla* at mid elevations; and *Gaultheria shallon* and *Polystichum munitum* at lower elevations (Fig. 7d).

Multi-response permutation procedures (MRBP) revealed significant differences in the composition of UB–B plot pairs in most contexts (Table 1), despite their proximity in ordination space. Composition differed in thinned and unthinned sites, and in the *Tsuga heterophylla* zone, but not in the *Abies amabilis* zone.

3.6. Relationships with burn severity, physical environment, and overstory structure

The direction and magnitude of the understory burn effect (B – UB difference) varied widely among sites (Fig. 8), and relationships with predictors were either non-significant (forest herb model) or weak (all other models) (Table 2). In all instances, models explained <25% of the variation in the response.

Burn severity was a significant predictor in two models (Fig. 8a; Table 2). For forest sub-shrubs, increasing severity of fire appeared to temper the negative effect of burning (mostly negative values but a positive slope; Fig. 8a). In contrast, for forest low shrubs, the response to burning shifted from neutral at low severity to mostly negative at higher severity (Fig. 8a).

Measures of site environment (heat load and elevation) were significant predictors in two models (Fig. 8b; Table 2). For total cover of forest species, heat load amplified the negative effect of burning (negative slope; Fig. 8b). For forest low shrubs, the burn effect shifted from negative to positive with elevation (Fig. 8b).

Measures of the difference in overstory structure between B and UB plots were significant in four models (Fig. 8c; Table 2). For early-seral species, the positive response to burning was enhanced when canopy cover was lower in B than in UB (mostly positive values but a negative slope; Fig. 8c). In contrast, lower canopy cover in B than in UB tempered

the negative response to burning in forest sub-shrubs (mostly negative values and a negative slope; Fig. 8c) but constrained the recovery of forest tall shrubs (mostly negative values but a positive slope) (Fig. 8c). Finally, greater basal area in B than in UB constrained the recovery of forest species in general, and forest tall shrubs in particular (Fig. 8c).

4. Discussion

For much of the 20th century, broadcast burning of logging residues was used as a tool for silviculture and fuels-management in the Pacific Northwest (Agee, 1989). Although approaches to harvesting and treatment of woody residues have changed considerably, legacies of past management remain prominent in the landscape. Key among these are the loss or fragmentation of old-growth forests and their replacement by younger, structurally simpler stands. Within this broader ecological context, we explored whether burning of logging slash leaves an imprint in the understory as regenerating forests transition from open- to closed-canopy stands. We asked three questions: First, can we detect legacies of burning four decades after harvest and, if so, which community attributes are most sensitive to burning? Here, we found persistent effects of burning ranging from subtle differences in the cover of early-seral species to marked reductions in the cover of residual tall shrubs. However, other aspects of community structure (e.g., herb cover and species diversity) were unaffected by burning. Second, we asked whether pre-commercial thinning, conducted two to three decades after harvest, altered responses to burning. Here, we found that thinning tempered effects of burning for some community attributes (species richness, evenness, and composition), but it had a compounding or amplifying effect for others (cover or variation in cover of residual tall shrubs). Finally, we asked whether the direction or magnitude of the burn effect—which varied widely among sites—could be explained by variation in burn severity, site environment, or overstory structure. Here, we found consistently weak relationships, underscoring the challenge of predicting long-term responses to fire at a local scale.

4.1. Seral groups and growth forms

Four decades after logging and burning, early-seral species contributed minimally to the vegetation. However, they remained nearly twice as abundant in burned as in unburned plots, despite comparable overstory development. Fire initially favors early-seral species by creating mineral seed beds, triggering germination from the seed bank, and reducing competition (Brodie et al., 2021; Grime, 1977). These species can remain prominent for one to two decades after burning, with dominance shifting from shorter-lived herbaceous to longer-lived woody species (Halpern and Franklin, 1990; Halpern and Lutz, 2013; Schoonmaker and McKee, 1988). In the absence of burning, however, dominance may revert more rapidly to residual forest species (Halpern, 1988; Halpern and Franklin, 1990). Although the transition to dominance by forest species occurred decades earlier at most of our sites (Kraemer, 1977; Morris, 1970), we still detected a legacy of burning in the elevated abundance of early-seral species. Surprisingly, this pattern was not driven by the more common taxa, including classic fire-followers such as *Chamerion angustifolium* or *Ceanothus velutinus* (Anderson, 2001; Conard et al., 1985; Pavek, 1992). All of the common species showed neutral responses to burning, including *Ceanothus*, which had been far more abundant on burned plots in earlier measurements (Kraemer, 1977; Morris, 1970). Rather, the persistence of an early-seral burn effect reflected the cumulative response of a regionally diverse, but locally sparse, pool of colonists. Indeed, burned plots supported an average of only three early-seral species, and nearly 80% of these occurred in fewer than 20% of the sites (Table A2, Appendix A).

Although early-seral species were typically more abundant in burned plots, there was considerable variation among sites in the magnitude of the burn effect. Although burn severity can dictate early-seral abundance in the short term (Halpern and Spies, 1995; Schimmel and

Table 1

Results of multi-response permutation procedures (MRBP[a]) testing for differences in species composition between burn treatments (UB vs. B) in differing contexts. Tests were conducted for all sites and for sites representing each thinning history and major forest zone. Significance ($P \leq 0.05$) is indicated by bold font.

Context	n[b]	T[c]	A[d]	P[e]
All sites	88	-6.922	0.0219	**<0.0001**
Thinned sites	54	-4.539	0.0240	**0.0004**
Unthinned sites	34	-2.388	0.0217	**0.022**
Tsuga heterophylla zone	64	-6.699	0.0315	**<0.0001**
Abies amabilis zone	18	-0.576	0.0094	0.25

[a] A blocked variant of MRPP, accounting for the pairing of plots at each site.
[b] number of plots (twice the number of sites).
[c] Test statistic (T) computed as ($\delta_{observed}$ - $\delta_{expected}$)/standard deviation of $\delta_{expected}$, where δ is the weighted-mean within-group distance.
[d] Chance-corrected with-group agreement (A), or effect size computed as $1 - (\delta_{observed}/\delta_{expected})$. The maximum value of A is 1.0 (when all samples within groups are compositionally identical). A is 0 when heterogeneity within groups equals the expectation by chance and A is negative when heterogeneity within groups is greater than expected by chance.
[e] Probability (P) of obtaining a δ as or more extreme than the $\delta_{observed}$ given the distribution of possible δs.

Fig. 8. Relationships of the understory burn effect (difference in cover between B and UB) with (a) burn severity, (b) site environment (heat load or elevation), and (c) overstory structure (difference in canopy cover or basal area between B and UB). Full set of results from stepwise regression models are presented in Table 2. Points above the horizontal dashed lines represent sites with greater understory cover in B than in UB. Points to the right of the vertical dashed lines represent sites with greater overstory development in B than in UB. Marginal significance (0.05 < P ≤ 0.1) is indicated by an underscore. Sites are coded by thinning history.

Granstrom, 1996; Wang and Kemball, 2005), it did not emerge as a significant predictor of cover in the longer term. This is not surprising given that the short-term responses of this group are driven by annuals and short-lived perennials (Halpern, 1989; Stevens et al., 2015), which were uncommon after four decades. However, we did find a significant (albeit weak) relationship with overstory development: early-seral cover was greater where burned plots remained more open than unburned plots—a pattern consistent with the shade intolerance of most early-seral species (Bazzaz, 1979; Halpern, 1989; Henry and Aarssen, 1997).

Pre-commercial thinning appeared to compound the effect of burning on early-seral species, increasing cover nearly four-fold

Table 2

Results of stepwise regression models exploring sources of variation in the magnitude of the understory burn effect (difference in cover between burn treatments, B – UB). Seven predictors (burn severity and measures of the physical environment and stand structure) were tested in each of six models of understory response. Relationships between response variables and significant predictors are shown graphically in Fig. 8.

Response variable (B – UB)	Burn severity[b]	Environmental variables			Structural-difference variables[a]			Model fit	
		Latitude	Elevation	Heat load[c]	Canopy cover	Total density	Total basal area	Adjusted R^2	RMSE[d]
Early-seral species cover (%)								0.224	11.68
Coefficient	…	…	…	…	–0.35871	…	…		
(SE)	…	…	…	…	(0.09896)	…	…		
P	…	…	…	…	0.0008	…	…		
Forest species cover (%)								0.166	21.71
Coefficient	…	…	…	–36.989	…	…	0.89459		
(SE)	…	…	…	(17.5977)	…	…	(0.40574)		
P	…	…	…	0.042	…	…	0.033		
Forest herb cover (%)[e]								—	—
Forest sub-shrub cover (%)[f]								0.230	1.59
Coefficient	0.0448	…	…	…	–0.0349	…	…		
(SE)	(0.0134)	…	…	…	(0.0137)	…	…		
P	0.0019	…	…	…	0.015	…	…		
Forest low shrub cover (%)								0.196	12.65
Coefficient	–0.2069	…	0.0261	…	…	…	…		
(SE)	(0.1041)	…	(0.0089)	…	…	…	…		
P	0.054	…	0.005	…	…	…	…		
Forest tall shrub cover (%)								0.153	14.73
Coefficient	…	…	…	…	0.2693	…	–0.8092		
(SE)	…	…	…	…	(0.1307)	…	(0.2875)		
P	…	…	…	…	0.046	…	0.007		

[a] Difference in canopy cover, density, or basal area between burn treatments (B – UB).
[b] Percentage of the ground surface rated as moderately to severely burned (see Section 2.2).
[c] An index of potential direct incident radiation and temperature derived from slope, aspect, and latitude (McCune and Keon, 2002).
[d] Root mean square error (standard deviation of the residuals).
[e] Relationships were non-significant.
[f] Cube-root transformation of the response variable.

compared to plots that remained unburned and unthinned. Species' models suggest that this thinning effect was driven by the vegetative expansion of *Pteridium aquilinum,* which was present at a majority of the sites. *Pteridium* is strongly clonal, maintaining a system of deeply buried rhizomes and dormant buds from which it can expand following partial or complete removal of the canopy (Fletcher and Kirkwood, 1979; Haeussler and Coates, 1986; Halpern and Antos, 2022).

All woody forest growth forms, including sub-shrubs, low shrubs, and tall shrubs, showed reduced cover in burned plots, suggesting that burning can affect understory physiognomy for decades after harvest (Halpern and Franklin, 1990). In the absence of pre-harvest data, it is less clear whether these burn effects also imply incomplete recovery from disturbance. Studies that have included a pre-harvest baseline suggest that these apparent reductions in cover may reflect the release of woody species in unburned plots, not the lack of recovery in burned plots (Halpern and Franklin, 1990; Halpern, unpublished data).

Forest tall shrubs showed stronger responses to burning than did shorter-statured woody species (i.e., forest sub-shrubs and low shrubs). Recovery from fire is often slowest in taller woody species, reflecting the time required to replace woody biomass (Halpern and Franklin, 1990; Kayes et al., 2010; Schoonmaker and McKee, 1988). Species within this group also showed fairly consistent responses to burning, although much of the reduction in cover was attributable to the dominants, *Acer circinatum* and *Rhododendron macrophyllum. Rhododendron* appeared particularly sensitive to burning, with absence from the burned plots at some sites suggesting local extirpation by fire (Table A2, Appendix A). *Rhododendron*'s greater susceptibility to burning likely reflects its more exposed root crown and shallower root system (Duchac, 2021; Dunn, 2015; Halpern and Antos, 2022).

Forest tall shrubs also responded negatively to thinning. As a result, the cumulative effects of thinning and burning were dramatic—reducing total cover by 50% relative to plots that received neither treatment.

Although cover may have been depressed prior to pre-commercial thinning (as stands targeted for thinning are typically denser), the decline on thinned sites more likely reflects the physical damage (stem breakage or crushing) incurred during felling. Recovery from thinning damage can take 5–10 years or more (Ares et al., 2010; Chan et al., 2006; Davis and Puettmann, 2009), and can be slowed by rapid crown expansion in *Pseudotsuga* (Bailey et al., 1998; Chan et al., 2006; Thomas et al., 1999). Indeed, post-thinning closure of the tree canopy was fairly rapid in this study: although tree densities were reduced by ~40%, thinned sites had regained canopy cover comparable to unthinned sites in little over a decade. Cover of tall shrubs also declined across the 20-year chronosequence of thinned sites, suggesting an inhibitory effect of crown expansion.

Burning had more subtle effects on shorter woody growth forms. In this system, the principal low shrubs, *Gaultheria shallon* and *Mahonia nervosa,* are top-killed by burning, but can resprout from well-developed systems of roots and rhizomes, if burning is not too severe (Haeussler and Coates, 1986; Halpern and Antos, 2022; Tirmenstein, 1990a, 1990b). *Gaultheria* appeared more sensitive to burning, consistent with its shallower rhizome system, which is often concentrated at the humus-mineral soil interface (Huffman et al., 1994; Huffman and Tappeiner, 1997). Previous studies suggest that both species can regain their pre-harvest abundance within two to three decades, or earlier in the absence of burning (Halpern, 1989; Halpern, unpublished data; Schoonmaker and McKee, 1988). Results of our regression analyses are consistent with these patterns: low shrubs were less abundant in plots that burned at higher severity and in higher-elevation (lower-productivity) sites, where growth was likely to have been slower.

Forest sub-shrubs, which invest little in woody biomass, were less sensitive to burning than were low or tall shrubs. Although most species of sub-shrubs were unaffected by fire, large declines in the dominant, *Linnaea borealis,* drove the group response. *Linnaea*'s shallow root

system and surficial stolons make it highly susceptible to fire (Bradley, 1984; Ingersoll and Wilson, 1990; McLean, 1969), but where it survives, stoloniferous growth allows for vigorous clonal expansion (Halpern, 1989; Howard, 1993; Stickney, 1981; Whittle et al., 1997). Although the burn × thin interaction was non-significant for *Linnaea*, trends in cover were consistent with this trade-off between survival and growth: cover was reduced in burned plots but enhanced by thinning in unburned plots. The remaining sub-shrubs, which appeared more resilient to fire, have various strategies for survival. Some resprout from more deeply buried taproots (e.g., *Rubus ursinus*; Morgan and Neuenschwander, 1988; Tirmenstein, 1989) or rhizomes (e.g., *Cornus canadensis*; Chapman and Crow, 1981; Flinn and Wein, 1977). Other stoloniferous species, such *Whipplea modesta,* are susceptible to burning (Halpern, 1989; Halpern and Antos, 2022), but maintain a viable seed bank that contributes to post-fire recruitment (Antos and Halpern, 1997). However, all share a common trait—the ability to spread clonally when resource conditions improve (Gucker, 2012a; Halpern, 1989; Tirmenstein, 1989). Results from our regression models were consistent with this trait: sub-shrub responses to burning were tempered where overstory conditions were more open.

In contrast to the woody growth forms, forest herbs were unaffected by burning. In fact, total cover was as likely to increase as to decline in burned plots. Others have attributed this neutral or varying response to fire to the offsetting effects of trait variation in the herb layer (Abella and Springer, 2015; Kerns et al., 2006; Rossman et al., 2018; Webster and Halpern, 2010; Willms, et al., 2017). In our study, this variation reflects both the regional scope of sampling (encompassing broad gradients in herb composition) and the coarse level at which we grouped species. Greater predictability could be achieved with finer groupings based on species' root-system traits (Antos and Halpern, 1997; Klimešová et al., 2021; Thomas et al., 1999), physiological constraints (Nelson et al., 2007), or seral affinities (e.g., generalist vs. late seral; Halpern et al., 2012; Lindh and Muir, 2004; McKenzie et al., 2000; Moola and Vasseur, 2004). For example, the negative responses to burning in *Tiarella trifoliata* and *Pyrola* spp. (Table A2; Appendix A) are consistent with their affinities for late-seral forests (Halpern and Spies, 1995). On the other hand, it is difficult to explain the greater abundance of *Trientalis* and *Viola* spp. in burned plots. Their responses to fire suggest a more complex long-term dynamic. Given the variation in species' responses to burning, it is not surprising that we were unable to relate the group response to variation in burn severity, site environment, or stand structure.

In contrast to burning, thinning greatly enhanced the cover forest herbs, despite subsequent closure of the tree canopy. This decoupling of understory and overstory responses to thinning has been attributed to the lagged response of the herb layer to changing resource conditions (Thomas et al., 1999). Clonal forest herbs can respond rapidly to sudden increases in light following thinning (Bailey et al., 1998; Halpern, 1989; Lindh et al., 2003), but their declines are more gradual as the canopy closes (Alaback and Herman, 1988; Lindh and Muir, 2004; Thomas et al., 1999). As a result, effects of thinning can persist in the understory long after those in the canopy have disappeared. Indeed, in this study, herb cover appeared to increase as canopy cover declined across the 20-year chronosequence of thinned sites.

4.2. Measures of diversity and within-plot variation

We were unable to detect effects of burning on most other attributes of community structure, but where we did, they were weak or contingent on thinning history. For example, burning had a small, but significant, effect on the richness of early-seral species in unthinned sites, but it had no effect on the richness of forest species. Comparable studies of somewhat shorter duration suggest that forest species can regain or surpass their pre-harvest richness within two decades of burning (Halpern and Spies, 1995). Thus, in the current study, it is likely that burned plots had recovered, if not exceeded, their pre-harvest richness. Two

factors contribute to the post-fire resilience of these forest understories: the capacity of most species to withstand moderate-severity fire (Haeussler and Coates, 1986; Halpern, 1989; Volland and Dell, 1981) and the patchy nature of broadcast burning, resulting in localized survival. In this study, moderate-severity fall burns left a mosaic of burned and unburned microsites (Morris, 1958, 1970)—the latter serving as sources of seed dispersal and vegetative expansion. Our inability to detect an effect of burning on forest species richness could be an artifact of plot size; however, results were similar for subplot-scale richness, suggesting comparable species' density at smaller spatial scales. Similarly, species diversity, which is less sensitive to the presence of uncommon taxa, was unaffected by burning. In contrast, burning had a persistent effect on the distribution of abundance among species—concentrating cover among fewer taxa—but only in unthinned sites. Thinning appeared to erase this effect. Two dynamics likely contributed to these outcomes: a shift toward dominance by fire-tolerant species in burned plots, and the release of strongly clonal species (e.g., *Pteridium aquilinum* and *Rubus parviflorus*) in response to thinning (Fletcher and Kirkwood, 1979; Gucker, 2012b; Haeussler and Coates, 1986; Halpern and Antos, 2022).

We also considered the effects of burning on the spatial heterogeneity of plant cover within plots—an indicator of habitat diversity and its related ecological functions (Christensen, 1997; Fuhlendorf et al., 2006; Wiens, 1997). Although understory heterogeneity is assumed to develop in parallel with canopy complexity (Franklin et al., 2002; Halpern and Spies, 1995; Stewart, 1988), it may also arise earlier as a consequence of uneven burning (Agee, 1993; Shafi and Yarranton, 1973b) or the patchy establishment of trees (Donato et al., 2009, 2012; Dunn et al., 2020; Shatford et al., 2007). Any evidence that burning promoted understory heterogeneity was limited to the tall-shrub layer, and only in thinned sites. Here, the combined effects of burning and thinning increased spatial variability while reducing total cover. Otherwise, thinning appeared to have an homogenizing effect, reducing the variability in herb-layer cover and increasing the compositional similarity of subplots. As with evenness, these effects were likely driven by the vegetative expansion of clonal species in response to resource enrichment (Haeussler and Coates, 1986; Huffman et al., 1994). Clearly, our ability to generalize about spatial heterogeneity in the development of the forest understory is constrained by the size and spacing of subplots in this study. The spatial patterning of fire effects and post-fire responses may differ at larger or smaller scales (Addicott et al., 1987; Rice, 1993; Wiens, 1989).

4.3. Compositional responses

As with many other attributes of the understory, burning had subtle, but persistent effects on species composition. After four decades, paired burned and unburned plots were distinguishable, even in thinned sites. That said, thinning did reduce the dissimilarity of plot pairs, as it did at among subplots within plots. It appears that the same process, the post-thinning expansion of strongly clonal species, can promote compositional convergence at a range of spatial scales.

In contrast to these differences within sites, we were unable to distinguish the larger set of burned from unburned plots, as local effects of burning were masked by stronger compositional gradients associated with elevation and latitude. Although structural vectors in the ordination space also suggested strong controls of overstory on understory composition, a simpler explanation is that both vary in parallel with elevation and latitude: sites in the *Abies amabilis* zone support a distinctive, higher-elevation flora, but they are also less productive and slower to develop structurally. Surprisingly, we were unable to detect a compositional response to burning in the *Abies amabilis* zone, despite the slower pace of structural development. Two factors likely contributed to this result. First, higher-elevation sites tended to burn at lower severity (Miller et al., 1990), likely tempering the initial effects of burning. Second, site replication was much lower, reducing the power to detect a

compositional response to burning.

5. Conclusions and management implications

Recent decades have seen major shifts in the management of public forestlands in the Pacific Northwest (Franklin and Donato, 2020; Swanson and Franklin, 1992). Currently, fire plays a minor role in the management of west-side forests in this region. Here, the focus has shifted from regeneration harvesting of mature and older stands to thinning of younger stands, which generate considerably less slash. Nevertheless, large portions of the landscape continue to recover from a history of logging and broadcast burning. Our 40-year assessment of the Morris plots broadens both the geographic scope and timeframe over which burning effects have been considered. It reveals persistent, but mostly subtle, effects of burning for many aspects of community structure, but more generally, it underscores the resilience of a flora adapted to infrequent, moderate- to high-severity fire (Morrison and Swanson, 1990; Tepley et al., 2013; Weisberg and Swanson, 2003).

Despite four decades of forest recovery, species that characterize early-seral habitats were more numerous and abundant in burned plots, particularly where canopy closure was delayed. This suggests that, where it is feasible to use fire in conjunction with regeneration harvesting, e.g., within aggregated-retention units (Franklin et al., 2019; Keyes et al., 2014; Koivula and Vanha-Majamaa, 2020; Scott et al., 2015), it may be possible to extend what is typically a transient, but biologically rich, phase of forest development—one that has been reduced by decades of intensive forest management and fire suppression (Kennedy and Spies, 2005; Swanson et al., 2011).

We observed stronger legacies of burning among woody components of the forest understory. Tall shrubs, a prominent structural element of these forests, were most sensitive to burning, reflecting their long-term investment in woody biomass. Late-seral herbs, although poorly represented in this study, may be even slower to recover due to their inherently sparse distributions, limited seed production (Meier et al., 1995), poor dispersal (Bierzychudek, 1982; Cain et al., 1998; Ehrlén and Eriksson, 2000), dependence on mycorrhizal symbionts (Rasmussen, 1995; Whigham, 2004), and narrow habitat requirements (Nelson et al., 2007). In fact, their persistence in the managed forest landscape may hinge as much on the recency or frequency of logging, as on the occurrence of fire itself (Halpern and Spies, 1995).

In this study, effects of pre-commercial thinning need to be viewed with caution due to the possible confounding of thinning history with site environment and vegetation. Nevertheless, they suggest how silvicultural practices that enhance tree growth can alter or compound prior effects of burning in the understory. Interactive effects, in which responses to burning were tempered or amplified by thinning, were fairly subtle and limited to measures of diversity or within-plot variation. However, effects of thinning were more dramatic where they compounded the effects of burning. Compared to plots that received neither treatment, thinning of burned plots resulted in nearly four times the cover of early-seral herbs, but half the cover of forest tall shrubs. For managers, this suggests that knowledge of prior disturbance could be useful in predicting site-specific responses to thinning. These types of 'compound-disturbance effects', where repeated perturbations amplify responses to, or limit recovery from, disturbance, are receiving increasing attention as climate warming and other anthropogenic pressures alter the frequency and vulnerability of systems to disturbance (Buma and Wessman, 2012; Burton et al., 2020; Kleinman et al., 2019). Our data suggest that, in forests that evolved with infrequent fire, relatively short intervals between burning and thinning can limit the recovery of a key structural element of the forest understory. Similar or more extreme effects have been described for systems in which the frequency of burning has exceeded that of the historical fire regime. These effects range from reductions in species' abundance or reproductive output (Enright et al., 2015; Halpern and Antos, 2022), to changes in taxonomic or functional composition (McCord et al., 2019;

Duivenvoorden et al., 2024; Kiel et al., 2023), to novel shifts in ecosystem state (Coop et al., 2020; Johnstone et al., 2016).

The broad spatial and temporal scope of this study make it possible to generalize about the nature and longevity of burn effects in west-side forests of this region. The overarching similarity of plot pairs highlights the resilience of a system that has evolved with infrequent, moderate- to high-severity fire. Yet, this local pairing of plots also reveals marked variation in the response to burning—variation that is not easily explained by simple descriptors of burn severity, site environment, or stand structure. Our limited ability to model this variation points to one or more possibilities. First, our simple, static regression models can't capture the complex, time-dependent influences and interactions among overstory and site attributes. Second, there are many relationships that we haven't considered, including biotic interactions in the understory (e.g., competition among growth forms), and historical or stochastic factors that can alter understory development independent of fire (Halpern, 1989; Miller and Safford, 2020; Romme et al., 2016). Finally, our ability to interpret variation in the burn effect hinges on the assumption that plot pairs shared a similar composition and structure prior to harvest. Given the strong dependence of the understory on vegetative recovery, any deviation from this assumption could give the appearance of divergence in composition or structure. This underscores the critical importance of pre-harvest data as a basis for assessing responses to, and recovery from, fire.

Twentieth-century logging of Pacific Northwestern forests has led to the landscape-scale replacement of old, structurally complex forests with young, structurally simpler stands. Relative to the effects of clearcut logging and the conversion of older to younger forests, the consequences of broadcast burning appear minor. Although the use of fire in forest management has changed dramatically in the last century, our study of vegetation responses to historical burning practices can inform its future application. Our results suggest that where it is operationally feasible, controlled burning can be used in conjunction with regeneration harvesting to achieve a variety of management objectives, with mostly subtle effects on the forest understory.

CRediT authorship contribution statement

Halpern Charles B.: Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft. **Lezberg Ann L.:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Bigley Richard E.:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – review & editing.

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.

Data availability

Data will be made available on request.

Appendix A

Table A1

Site characteristics and management history of the 44 study sites, ordered from north to south. Slope is the average of unburned (UB) and burned (B) plots (typically <5% difference). If aspects differed between UB and B, both are listed. Primary overstory species are ordered by relative abundance in the unburned plot. Nomenclature and species codes are from the USDA Plants database (USDA and NRCS, 2021).

Site name	Forest zone[1]	Elevation (m)	Slope (%)	Aspect (UB, B) (deg)	Primary overstory species[2]	Management history[3]
Huckleberry Creek 4	Tshe	762	60	344	Psme	T, F
Huckleberry Creek 6	Abam	1006	39	64	Psme, Tshe	T
Willame Creek 13	Abam	991	40	180	Abam	T
Davis Creek South 2	Abam	975	19	290, 282	Psme, Tshe, Abam	T
Davis Creek North 2	Abam	975	43	260, 270	Abam, Psme	T
Trout Creek 4	Tshe-Abam	549	12	150, 215	Tshe, Psme, Abam	T, P
Panther Creek	Tshe	488	31	240	Psme, Pipo	T, P
Cougar Rock North	Abam	823	35	110	Abam, Psme	T, F
Fish (First) Creek	Tshe	701	20	260, 300	Psme	T, P
Pup Creek	Tshe	878	7	340, 335	Tshe	T
John's Creek P1	Tshe	1128	14	335, 305	Psme, Tshe	T, F
Upper Mag Creek	Tshe	884	30	246, 280	Psme	T
Big Creek	Tshe	640	12	250	Psme	T
Divide Creek 7	Tshe-Abam	1219	34	290, 300	Psme	T, F
Divide Creek 6 North	Tshe-Abam	1036	30	310	Psme	T, P
Divide Creek 6 South	Abam	1067	17	10	Tabr2, Abam	T
Rainbow Lake	Tshe	957	47	350	Psme	T, F
South Fork Springfield 4	Tshe	701	9	5, 70	Psme	T
H. J. Andrews 1-C	Tshe	579	12	320, 205	Psme, Chch7	T, P
Andy Creek 2	Tshe	579	13	48, 14	Psme, Tshe	T, F
Andy Creek 3	Tshe	838	19	60, 53	Psme	F
Gurrier 7	Tshe	1067	13	313, 322	Psme	
Gurrier 9	Tshe	1067	8	20, 330	Psme	
Gurrier 2	Tshe	427	26	170, 210	Psme	T, F
Spar 30	Tshe	1021	10	20	Psme	
Spar 31	Tshe	1128	15	280	Chch7, Psme, Tabr2	F
Spar 40	Tshe	1113	18	265, 310	Psme, Chch7	F
Christy Creek J	Abam	1029	10	140, 130	Psme	F
Christy Creek K	Abam	963	0	—	Psme	
Salmon Creek 6	Tshe	884	5	250, 182	Psme	F
Salmon Creek 8	Tshe	899	29	195	Psme	
Salmon Creek 11	Tshe	975	4	270, 230	Psme	F
Salmon Creek 14	Tshe	945	9	150, 180	Psme	T,P
Wheeler-Osgood	Tshe	792	30	140	Psme, Tshe	T, P
Bohemia Unit 4	Tshe	732	55	300	Psme	T, P
Associated Plywood 1	Tshe	594	65	162, 195	Psme	T, F
Associated Plywood 5	Tshe	823	9	90, 140	Psme	P
Emile Creek 1 Upper	Tshe	991	5	60, 50	Psme	T, P
Emile Creek 3 Lower	Tshe	945	20	40, 340	Psme, Thpl	T, P
South Myrtle Creek P1	Abam	1143	30	250	Chch7, Psme	P
South Myrtle Creek P2	Tshe	1158	31	300, 280	Tshe	P
Bear Camp 1-P1	Abam	1158	10	350, 330	Psme, Abam	
Bear Camp 2-P3	Abam	1280	14	70	Psme, Abgr	P
Woods Creek	Tshe	427	78	140, 130	Psme	P

[1]Abam = *Abies amabilis* zone, Tshe = *Tsuga heterophylla* zone, Tshe-Abam = transitional between *Tsuga* and *Abies* zones.

[2]Abam = *Abies amabilis*, Abgr = *Abies grandis*, Chch7 = *Chrysolepis chrysophylla*, Pipo = *Pinus ponderosa*, Psme = *Pseudotsuga menziesii*, Tabr2 = *Taxus brevifolia*, Thpl = *Thuja plicata*, Tshe = *Tsuga heterophylla*.

[3]T = pre-commercially thinned, P = planted, F = fertilized.

Table A2

Occurrence (% of sites and plots) and mean cover of all understory taxa arranged by seral group and growth form. Within each group, species are arranged in descending order of occurrence (% of sites). Mean cover is based on 27 thinned or 17 unthinned sites; species values in Figs. 4–6 are based on sites in which a species occurred. Blank cells indicate absence from all pairs of unburned (UB) and burned (B) plots. Plant nomenclature follows the USDA Plants Database (USDA and NRCS, 2021). USDA plant codes are included for taxa plotted in the NMS ordination (Fig. 7).

Seral group: Growth form *Taxon*	Plant code	% of sites	Thinned sites (n = 27)				Unthinned sites (n = 17)			
			% of plots		Cover (%)		% of plots		Cover (%)	
			UB	B	UB	B	UB	B	UB	B
Early seral: Herbs		89	81	85	3.6	5.9	47	71	1.5	3.0
Pteridium aquilinum	Ptaq	66	59	70	3.0	4.9	24	35	0.7	1.4
Chamerion angustifolium	Chan9	36	37	26	0.5	0.4	18	24	0.8	0.9
Lupinus latifolius		18	11	11	<0.1	0.1	6	18	<0.1	0.2
Fragaria spp. (*F. vesca, F. virginiana*)		16	11	11	<0.1	0.1	0	18	0	0.1

(continued on next page)

Table A2 (*continued*)

Seral group: Growth form *Taxon*	Plant code	% of sites	Thinned sites (*n* = 27)				Unthinned sites (*n* = 17)			
			% of plots		Cover (%)		% of plots		Cover (%)	
			UB	B	UB	B	UB	B	UB	B
Anaphalis margaritacea		14	15	7	0.1	0.3	6	6	<0.1	<0.1
Stachys mexicana		9	4	11	<0.1	<0.1	6	6	<0.1	<0.1
Hypericum perforatum[1]		7	0	4	0	0.1	0	12	0	0.3
Claytonia spp.[2] (*C. sibirica, C. perfoliata*)		5	0	4	0	<0.1	6	0	<0.1	0
Antennaria sp.		2	4	4	<0.1	<0.1				
Apocynum androsaemifolium		2	4	4	<0.1	<0.1				
Senecio sylvaticus[1,2]		2	0	4	0	<0.1				
Stellaria calycantha		2	0	4	0	<0.1				
Equisetum sp. (*E. arvense* or *E. telmateia*)		2	4	0	<0.1	0				
Tussilago farfara[1]		2	4	0	<0.1	0				
Early seral: Tall shrubs		75	63	56	3.4	4.1	47	88	2.4	8.1
Rubus parviflorus	Rupa	46	41	44	2.3	2.5	35	41	1.2	0.4
Sambucus spp. (*Sambucus nigra* ssp. *cerulea, S. racemosa*)	Sambu	32	19	15	0.1	0.1	12	29	0.3	0.3
Ribes spp.	Ribes	27	15	26	0.4	0.4	24	24	0.6	0.2
Ceanothus velutinus	Ceve	20	4	4	0.2	0.5	12	41	0.2	6.5
Rubus spectabilis		14	11	11	0.1	0.1	6	12	0.1	0.1
Salix spp.		14	4	11	0.3	0.5	6	18	<0.1	0.2
Arctostaphylos columbiana		14	4	4	<0.1	<0.1	6	24	<0.1	0.5
Early seral: Hardwoods[3]		16	11	19	0.3	1.2	0	6	0	<0.1
Prunus emarginata		16	11	19	0.3	1.2	0	6	0	<0.1
Forest: Herbs		95	100	100	12.8	14.0	76	88	8.0	9.6
Polystichum munitum	Pomu	71	82	70	7.0	5.7	41	47	3.0	4.5
Trientalis borealis ssp. *latifolia*	Trbol	55	56	48	0.5	0.9	18	47	0.3	0.4
Viola spp., (*V. sempervirens, V. orbiculata, V. glabella*)	Viola	52	30	44	0.2	0.5	29	47	0.6	0.7
Galium spp. (*G. triflorum, G. oreganum*)	Galiu	48	37	48	0.4	0.5	18	18	0.1	0.2
Liliaceae spp.	Liliac	39	30	22	0.2	0.3	35	35	1.3	0.8
Trillium ovatum	Trov	25	19	11	0.1	0.1	18	24	0.1	0.1
Tiarella trifoliata	Titr	25	15	11	0.2	0.1	29	12	0.4	0.1
Oxalis oregana		23	19	22	1.5	3.3	18	24	0.7	1.5
Xerophyllum tenax		23	19	22	0.8	0.9	6	24	0.2	0.4
Achlys triphylla		23	26	19	0.3	0.2	0	6	0	0.1
Pyrola spp.		23	22	11	0.2	<0.1	18	12	0.4	0.1
Clintonia uniflora		16	22	15	0.3	0.2	6	6	0.4	<0.1
Asarum caudatum		16	11	11	0.7	0.7	24	12	0.2	0.2
Vancouveria hexandra		14	0	11	0	<0.1	12	12	0.2	0.3
Lycopodium clavatum		11	11	11	0.2	0.3	6	6	0.2	0.1
Adenocaulon bicolor		11	0	7	0	<0.1	12	6	<0.1	<0.1
Thalictrum occidentale		9	7	4	0.1	0.1	6	12	<0.1	<0.1
Blechnum spicant		7	7	7	0.1	<0.1	6	6	<0.1	<0.1
Goodyera oblongifolia		7	4	4	<0.1	<0.1	6	0	<0.1	0
Gymnocarpium dryopteris		5	4	4	<0.1	<0.1				
Orchidaceae spp.		5	0	4	0	<0.1	6	0	<0.1	0
Athyrium filix-femina		5	4	0	<0.1	0	6	0	<0.1	0
Maianthemum dilatatum		2	4	4	0.1	<0.1				
Erythronium grandiflorum		2	0	4	0	<0.1				
Listera caurina		2	0	4	0	<0.1				
Polypodium glycyrrhiza		2	0	4	0	<0.1				
Campanula scouleri		2	0	4	0	<0.1				
Hieracium albiflorum		2	4	0	<0.1	0				
Dicentra formosa		2					0	6	0	<0.1
Forest: Sub-shrubs		98	100	93	16.1	11.3	94	94	15.4	14.1
Rubus ursinus	Ruur	93	89	74	2.7	2.4	71	88	4.2	3.9
Linnaea borealis	Libo3	82	82	63	10.8	6.6	77	65	6.5	5.3
Cornus canadensis	Coca13	43	37	37	1.7	1.4	41	35	1.8	0.9
Whipplea modesta	Whmo	30	11	19	0.4	0.3	29	35	1.7	3.2
Rubus nivalis		23	19	22	0.2	0.1	12	6	0.1	<0.1
Rubus pedatus		20	19	15	0.2	0.4	18	24	0.4	0.3
Chimaphila umbellata		16	7	4	0.1	0.1	24	18	0.7	0.4
Forest: Low shrubs		98	96	96	28.2	25.3	88	94	21.0	15.3
Mahonia nervosa	Mane2	91	93	89	10.4	9.8	77	77	7.0	6.3
Gaultheria shallon	Gash	66	67	74	16.9	14.6	47	35	11.7	6.4
Gaultheria ovatifolia	Gaov2	25	30	11	0.7	0.4	6	12	0.1	0.1
Paxistima myrsinites		23	15	19	0.2	0.5	24	24	2.3	2.5
Forest: Tall shrubs		100	100	100	24.3	15.2	100	100	30.3	24.6
Acer circinatum	Acci	80	67	67	10.5	6.8	94	82	12.7	11.1

Table A2 (*continued*)

Seral group: Growth form *Taxon*	Plant code	% of sites	Thinned sites (n = 27)				Unthinned sites (n = 17)			
			% of plots		Cover (%)		% of plots		Cover (%)	
			UB	B	UB	B	UB	B	UB	B
Vaccinium parvifolium	Vapa	68	67	63	2.9	2.0	47	47	2.0	0.7
Rhododendron macrophyllum	Rhma3	66	48	37	4.8	1.4	82	65	12.3	10.7
Rosa gymnocarpa	Rogy	41	37	30	0.4	0.4	18	12	0.3	0.1
Vaccinium ovalifolium	Vaov	36	30	19	1.2	0.5	24	41	2.2	1.0
Holodiscus discolor		18	19	15	0.3	0.4	0	12	0	0.8
Vaccinium membranaceum		16	22	22	4.0	3.5	6	6	0.3	0.2
Corylus cornuta var. *californica*		7	7	7	0.2	0.2	6	0	0.5	0
Menziesia ferruginea		2	4	4	0.1	<0.1				
Acer glabrum		2	0	4	0	<0.1				
Forest: Hardwoods[3]		61	48	37	2.3	1.1	35	47	2.9	3.5
Chrysolepis chrysophylla	Chch7	46	33	22	0.8	0.2	35	41	2.9	0.8
Acer macrophyllum		16	15	15	0.6	0.8	0	6	0	2.5
Cornus nuttallii		11	11	7	0.6	<0.1	0	6	0	0.2
Frangula purshiana		9	15	11	0.3	0.1				
Unclassified: Herbs		23	7	15	<0.1	0.2	29	12	0.8	0.3
Poaceae spp.		16	7	11	<0.1	0.2	18	12	0.6	0.3
Luzula spp. (*L. parviflora, L. campestris*)		5	0	4	0	<0.1	6	0	0.1	0
Osmorhiza berteroi		2					6	0	0.1	0
Unclassified: Sub-shrubs		11	4	7	<0.1	0.2	18	12	1.6	1.7
Penstemon spp.		7	0	4	0	<0.1	12	6	1.5	1.4
Clinopodium douglasii		5	4	4	<0.1	0.2	6	6	0.1	0.3
Unclassified: Low shrubs		34	22	30	1.2	2.2	18	35	0.5	1.0
Symphoricarpos hesperius	Syhe	34	22	30	1.2	2.2	18	35	0.5	1.0
Unclassified: Tall shrubs		30	26	19	0.7	0.1	12	18	0.1	0.6
Oemleria cerasiformis		16	15	4	0.2	<0.1	12	12	0.1	0.1
Sorbus sitchensis		9	7	11	0.1	0.1				
Amelanchier alnifolia		7	7	4	0.2	<0.1	0	6	0	0.5
Alnus viridis ssp. *sinuata*		5	7	0	0.2	0				
Unclassified: Hardwoods[3]		2	4	4	<0.1	0.1				
Betula occidentalis		2	4	4	<0.1	0.1				

[1]Non-native
[2]Annual or short-lived perennial
[3]Stems <4.1 cm dbh

Table A3

Results of mixed-effects models for thinned sites (n = 27) testing relationships with time since thinning (time) and burn treatment; site was treated as a random effect. Significance ($P \leq 0.05$) is indicated by bold font and marginal significance ($0.05 < P \leq 0.1$), by an underscore. For significant relationships with time since thinning, + or – indicate the direction of the effect.

Response variable	+ / –	Time since thinning	Burn treatment	Time × Burn
Aggregate measures of overstory structure				
Total density (trees ha^{-1})[1]	+	**0.024**	0.88	0.93
Conifer density (trees ha^{-1})	+	<u>0.099</u>	0.50	0.93
Hardwood density (trees ha^{-1})[1]		0.50	0.86	0.71
Total basal area (m^2 ha^{-1})[1]	+	**0.001**	0.84	0.82
Stand density index[2]	+	**0.002**	0.92	0.89
Canopy cover (%)	+	**0.002**	0.54	0.86
Dominant tree height (m)	+	**0.0007**	0.77	0.94
Understory attributes				
Early-seral species cover				
Total (%)[2]		0.84	**0.022**	0.11
Herbs (%)[2]		0.68	<u>0.083</u>	<u>0.073</u>
Tall shrubs (%)		0.90	0.37	0.80
Forest species cover				
Total (%)		0.20	**0.004**	0.87
Herbs (%)[1]	+	**0.033**	0.99	0.60
Sub-shrubs (%)[1]		0.39	<u>0.054</u>	0.39
Low shrubs (%)	+	<u>0.083</u>	0.30	<u>0.057</u>
Tall shrubs (%)[2]	–	**0.024**	**0.003**	0.79
Understory hardwoods (%)		0.48	0.12	0.98
Indices and components of diversity				
Total richness (species plot^{-1})		0.42	0.36	0.85

(continued on next page)

Table A3 (*continued*)

Response variable	+ / −	Time since thinning	Burn treatment	Time × Burn
Early-seral species richness (species plot^{-1})		0.51	0.17	0.86
Forest species richness (species plot^{-1})		0.62	0.16	0.56
Diversity (N$_1$)		0.40	0.75	0.73
Evenness ([N$_2$ − 1]/[N$_1$ − 1])		0.77	0.86	0.91
Measures of within-plot variation				
CV of herb-layer cover (%)^2	−	**0.033**	0.36	0.53
CV of tall shrub-layer cover (%)^2	+	<u>0.061</u>	**0.008**	0.29
Compositional heterogeneity within plots^3		0.18	0.70	0.79

[1]Log transformation of the response variable.

[2]Square-root transformation of the response variable.

[3]Mean Bray-Curtis dissimilarity among subplots.

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