



## Native and non-native understory vegetation responses to restoration treatments in a dry conifer forest over 23 years

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### ABSTRACT

Restoration of fire-prone forests is a common practice intended to increase resilience to wildfire, drought, and bark beetles. However, the long-term effects of restoration treatments on understory species, particularly non-native species, are poorly understood. We investigated long-term (23 years) effects of restoration treatments on native and non-native understory vegetation at the Lick Creek Demonstration-Research Forest, a ponderosa pine/Douglas-fir forest in western Montana, USA. Restoration treatments included shelterwood-with-reserves harvesting implemented alone or in combination with prescribed burning under either wet or dry conditions, plus a no-action control. Changes in understory vegetation cover and species richness (measured pre-treatment, 2, 3, 4, 5, 15, and 23 years post-treatment) were analyzed by growth form (forb, graminoid, and shrub) and origin (native vs. non-native) to test how understory dynamics respond to disturbance intensity. We also accounted for basal area of trees to consider how differential overstory conditions affected final treatment responses. Native vegetation cover responses followed predictable successional patterns: after initial declines by grasses and shrubs immediately after disturbance (43% and 40% reduction, respectively), all groups increased, peaked about five years after disturbance (74% greater than pre-treatment on average) and then generally declined to levels similar to pre-treatment. The magnitude of these changes was related to the disturbance intensity (i.e., cut-and-dry-burn > cut-and-wet-burn > cut-and-no-burn > control). For all native groups, variation in tree basal area at year 23 explained remaining differences among treatments. Non-native grasses and forbs followed similar overall trajectories, but cover of these groups increased immediately after treatment and rose more steeply to their peak five years post-treatment (12 times greater than pre-treatment on average), with differences persisting through year 23. While non-native cover responses in year 23 were negatively correlated with tree basal area, as seen for native taxa, overstory conditions alone did not fully account for differences between burned and unburned treatments. This suggests that effects of burning unrelated to tree regeneration favored non-natives. Nonetheless, in the last sampling year treatment-induced increases in non-native cover were modest, suggesting that after 23 years understory responses in this forest type were fairly resilient to restoration treatments. However, because forest structure and composition were reverting to pre-treatment conditions by year 23, retreatment may be necessary at intervals of <23-years in our system, which could exacerbate non-native responses. Results of our long-term experiment provide insight into how different forest restoration treatments and their timing may affect understory susceptibility to non-native plant invasion.

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## 1. Introduction

Restoring forest structure within dry, fire-prone forest types in the western United States has been a leading management goal in recent decades (Hessburg et al., 2015; Stephens et al., 2018). Euro-American settlement, and subsequent activities such as logging, grazing, and fire suppression, have caused structure and species composition in many of these forests to deviate from historical conditions, with higher tree densities and species composition skewed toward late-successional species (Covington and Moore, 1994; Hessburg et al., 2015). As a consequence, and in conjunction with a warming climate, wildfires have increased in intensity, severity, and magnitude over recent decades (Flannigan et al., 2009; Seidl et al., 2016). Policy makers and managers have responded to concerns over forest vulnerability to wildfire by shifting goals towards restoring forest resistance and resilience to fire in the United States and throughout the world (Wildland Fire Leadership Council, 2014; North et al., 2015). Although the restoration treatments are commonly implemented to reduce hazardous fuels (Fulé et al., 2001), the core idea behind these restoration treatments is emulating the forest structure and successional pathways created by natural disturbances and thereby move the forest ecosystem toward conditions that are more resilient to wildfire (Franklin et al., 2002; Ares et al., 2009). However, overstory restoration treatments are disturbances that can substantially disrupt understory plant communities and facilitate non-native species invasions (e.g., Collins et al., 2007; Abella and Springer, 2015). It is important to not only consider the implications of overstory restoration on understory structure and composition (Strahan et al., 2015; Matonis et al., 2016; Laughlin et al., 2017), but proactively plan understory metrics for diversity goals and effects of treatment on invasives. Yet, relatively few studies have considered the long-term effects of overstory restoration treatments on understory plant communities, including prevalence of non-native species (Kalies and Yocom Kent, 2016; Willms et al., 2017).

Dry forest restoration treatments often involve thinning, prescribed burning, or a combination of these actions (Agee and Skinner, 2005; Kolb et al., 2007; North et al., 2007). In ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests with historically frequent, low-severity fire, these treatments are often intended to modify forest structure, tree species dominance, and fuel loading (e.g., removing overstory fuels to reduce the probability of active crown fire spread and removing midstory ladder fuels and surface fuels to reduce the probability of crown fire initiation). Forest restoration treatments have typically been successful at recovering a fire-tolerant overstory composition and reducing short-term fire hazard (Stephens et al., 2009; Fulé et al., 2012). However, treatments vary in their efficacy, longevity, and disturbance intensity. For example, treatments that combine cutting with burning in dry ponderosa pine forests tend to be more effective than cutting alone at reducing tree biomass and fuel loads for longer time periods (Clyatt et al., 2017; Crotteau et al., 2018a, 2020; Hood et al., 2020). However, combined treatments intensify disturbance. Through such disturbance, restoration treatments can strongly disrupt understory vegetation (Gundale et al., 2005; Wayman and North, 2007; Dodson et al., 2008; Rago et al., 2020), and the most effective treatments for accomplishing management objectives aimed at promoting resilience to wildland fire, i.e., high intensity treatments comprised of combined tactics, may be of particular concern to understories in some systems (Nelson et al., 2008).

Understory vegetation plays a critical role in the forest ecosystem, providing important ecological functions such as nutrient cycling, site productivity, wildlife habitat, and biodiversity (Allen et al., 2002; Kerns et al., 2009; MacLean and Wein, 1977). Changes to the understory by intensive disturbance (including active management) may adversely impact the forest ecosystem by having long-lasting negative impacts on plant cover and species composition (Halpern, 1988; Gilliam, 2007; Kreyling et al., 2008). One particularly adverse consequence is an increase in non-native, invasive species. Non-native species can increase following management practices such as cutting and burning (e.g.,

D'Antonio, 2000; Keeley, 2006; Laughlin et al., 2008), especially along associated roads, skid trails, and burn piles (Gelbard and Belnap, 2003). Non-native species invasions are of particular concern following restoration because they threaten to disrupt the plant communities that treatments are aimed to restore and they can increase surface fuel loads (Kerns et al., 2020). A meta-analysis of understory vegetation responses to fire and thinning found that all but one paper reported only short-term (<5 years post-treatment) results (Willms et al., 2017). The one paper reporting longer-term responses, Nelson et al. (2008), was based on opportunistic chronosequences (see also MacKenzie et al., 2004). Since Willms et al. (2017) was published, several studies have started to report longer-term vegetation responses to restoration treatments and wildfire (Rossman et al., 2018; Kerns and Day, 2018; Strand et al., 2019; Crotteau et al., 2020). However, additional experimental studies using a replicated treatment design to track native and non-native vegetation patterns over decades from pretreatment conditions are needed, particularly for dry western forests.

Restoration treatments at the Lick Creek Demonstration-Research Forest in western Montana provide a unique opportunity to evaluate long-term impacts of forest restoration on understory vegetation in the dry, fire-prone forests of the northern Rocky Mountains. In 1991–1993, researchers established an experiment testing the effects of a shelterwood-with-reserves (i.e., partial overstory removal to regenerate a stand under the cover of residual trees) regeneration harvest in combination with prescribed burning on the restoration of fire-excluded ponderosa pine stands. These silvicultural treatments were primarily intended to reduce fuels and mitigate fire behavior as well as to restore historical stand conditions typified by open, multi-aged forests (Smith and Arno, 1999). An additional objective was to increase biodiversity of native understory species while minimizing establishment of non-native species. Non-native species such as *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek were present in the general study area prior to treatments, and there was a concern that treatments could have the unintended consequence of increasing non-native species. Restoration treatments varied in disturbance intensity from cut-and-no-burn (least intense of the treatments), to cut-and-wet-burn (more intense, with limited organic matter consumption), and cut-and-dry-burn (most intense of treatments because of low fuel moisture, with high organic matter consumption). We investigated understory vegetation responses up to 23 years following treatment using three metrics: cover by plant group, defined by species origin and growth form; species richness by group; and community composition. Our main objective was to compare these responses among treatments over time. We predicted that the magnitude of the response would correspond with the magnitude of the disturbance intensity. In addition, we examined the fine-scale relationship between final understory metrics (cover and species richness by group) and overstory tree basal area to consider to what extent variation in the latter might explain differences among treatments. As a long-term, replicated field experiment, this study provides unique and robust information regarding how common forest restoration treatments influence understory plant communities, including non-native plant invasions.

## 2. Methods

### 2.1. Study site

This study was conducted at the Lick Creek Demonstration-Research Forest (hereafter Lick Creek) in the Bitterroot National Forest of southwestern Montana, USA (46°5'N, 114°15'W; Smith and Arno, 1999). Lick Creek is 21 km southwest of Hamilton, Montana, and elevations range from 1300 to 1500 m with south-facing slopes of 0–30% (Clyatt et al., 2017). The mean annual temperature is 7 °C and precipitation is 400 mm; 27–50% of total precipitation falls as snow during winter, most of the remaining precipitation falls during spring and fall, whereas summers are generally dry (DeLuca and Zouhar, 2000; Gruell et al., 1982).

Soils are shallow to moderately deep, originating from granitic parent materials (Gruell et al., 1982). The soils are classified as Elkner Gravelly Loam, coarse-loamy, mixed, frigid, Typic Cryochrepts (DeLuca and Zouhar, 2000).

The primary habitat types at Lick Creek are in the Douglas-fir series (Pfister et al., 1977). Ponderosa pine (overstory) and Douglas-fir (mid-story and understory) are the principal tree species. Grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) are found sporadically throughout the stands (Smith and Arno, 1999; Clyatt et al., 2017). The historical fire regime in this area was characterized by low-intensity surface fire at 3–30 year return intervals (Arno, 1976; Gruell et al., 1982).

The silvicultural experiment was conducted in a second growth ponderosa pine/Douglas-fir forest that had not burned for at least 50 years (DeLuca and Zouhar, 2000). Silvicultural activities from the early 20th century into the 1960s regenerated and released “thrifty” new cohorts of ponderosa pine, but also stimulated the development of thriving Douglas-fir cohorts (Crotteau et al., 2018b). Restoration treatments consisting of shelterwood harvesting alone or in combination with prescribed burning (see below for details) were implemented to reduce fuels while favoring ponderosa pine in the overstory, promoting its recruitment in the understory, and reducing Douglas-fir regeneration (Smith and Arno, 1999). As documented in associated research from this study, overstory and understory conditions differed markedly among restoration treatments 23 years after treatment (Clyatt et al., 2017; Hood et al., 2020). In the final year of the study, mean tree biomass was nearly double in unburned compared to burned units, reaching 153% of pre-treatment levels (vs. 85–89% of pre-treatment levels for burned units), as driven by substantial Douglas-fir regeneration (Hood et al., 2020; Tepley et al., 2020). Treatments, particularly those including burning, also caused persistent reductions in biomass of forest floor woody debris and duff (Clyatt et al., 2017), some canopy fuel metrics (Hood et al., 2020), and enhanced tree growth and resilience to drought (Tepley et al., 2020).

## 2.2. Experimental design and data collection

In this study, we examined the effects of restorative shelterwood-with-reserves harvesting and burning on understory vegetation dynamics. We used twelve experimental units of 1.6 to 4.0 ha randomly assigned to one of four treatments (three replicates per treatment): no-action control (CO), cut-and-no-burn (NB), cut-and-wet-burn (WB), and cut-and-dry-burn (DB). Shelterwood harvesting took place in July–August 1992. Immediately prior to cutting, tree density and basal area of the 85-year-old second growth stands were 435 trees ha<sup>-1</sup> and 27 m<sup>2</sup> ha<sup>-1</sup>, respectively, with 72% of trees being ponderosa pine, and no differences among planned treatment types (Arno, 1999). The shelterwood harvests reduced tree density and basal area to 174 trees ha<sup>-1</sup> and 12 m<sup>2</sup> ha<sup>-1</sup>, respectively (Clyatt, 2016). Harvests restored forest structure by reestablishing low overstory densities that more closely resemble two nearby historical stands (reconstructed to 125–164 trees ha<sup>-1</sup> and 15.7–16.6 m<sup>2</sup> ha<sup>-1</sup>; Clyatt et al., 2016), and by regenerating a new cohort to create multi-aged stands as were historically prevalent. Trees were felled by chainsaw and skidded by a crawler tractor and winch yarder. All limbs and boles except tree top (15 cm diameter) were extracted from the harvest units.

Post-harvest broadcast burns were applied in May 1993 under two different burning windows. The WB treatment was designed for low fuel consumption; units were burned when duff and large woody fuel (>7.6 cm diameter) moistures were 50% and 100%, respectively. In contrast, the DB treatment was designed for high fuel consumption, and units were burned when duff and large woody fuel moistures were 16% and 30%, respectively (Smith and Arno, 1999). The prescribed burning consumed approximately 75% of litter and woody materials in the forest floor, and reduced duff depth by 17% and 38% for WB and DB,

respectively (Harrington, 1999). Fire-caused mortality was high for both burn treatments in the 2.5–17.8 cm diameter (at breast height) class; approximately 65% of trees (90% of which were Douglas-fir seedlings) in this size class were killed by burning, while only 6% of trees in this diameter class were dead in the unburned treatment (Harrington, 1999).

Understory vegetation in experimental units was measured once per growing season in each of seven years: 1991 (pre-treatment), 1994 (+2 years after initial cutting treatment), 1995 (+3 years), 1996 (+4 years), 1997 (+5 years), 2007 (+15 years), and 2015 (+23 years). Control units were only measured in 2007 and 2015. Within each experiment unit, a grid of 12 plot centers was installed at 15–40 m spacing depending on the size and shape of the unit, for a total of 144 plots. Four, 1 m<sup>2</sup> (0.7 m × 1.43 m) permanent understory vegetation plots (sub-plots) were established per sampling point (plot). The sub-plots were located 2.1 m from the sampling point along and perpendicular to the slope contour, with the sub-plot long axis oriented perpendicular to the slope. All understory vegetation species (including small trees, shrubs, forbs, and graminoids) were identified, and except in 2015, cover classes were visually estimated following Daubenmire’s (1959) protocol, which included seven cover classes (0–5%, 5–20%, 20–40%, 40–60%, 60–80%, 80–95%, and 95–100%). In 2015, we used the FIREMON inventory protocol (Caratti, 2006), which is similar to the Daubenmire protocol except with twelve cover classes (0–1%, 1–5%, 5–15%, 15–25%, 25–35%, 35–45%, 45–55%, 55–65%, 65–75%, 75–85%, 85–95%, and 95–100%). We used cover class midpoints for quantitative analyses (Gendreau-Berthiaume et al., 2015). To account for the class difference between inventory protocols, we used the midpoint of each FIREMON class to reassign 2015 measurements to Daubenmire classes. Understory species were assigned to groups defined by growth form (shrub, forb, and graminoid) crossed by origin (i.e., native vs. non-native). Tree species were not included given they have been the focus of prior studies addressing effects of these restoration treatments (Clyatt et al., 2017; Hood et al., 2020). Non-native shrubs were never observed in plots, which left five growth form × origin groups for analysis. For each group, we summed cover of constituent species per subplot and then averaged these values at the plot level for analysis. Similarly, species richness per group was represented by the number of unique species per plot.

In addition, forest conditions were measured throughout the study as part of related work (Clyatt et al., 2017; Hood et al., 2020). Diameter at breast height (dbh) was recorded for all trees taller than 137 cm in 0.04 ha circular plots (11.3 m radius) that were centered on the permanent sampling points. Basal area per tree was calculated from dbh, summed to the plot level, and then standardized to overstory basal area (m<sup>2</sup> ha<sup>-1</sup>). Nomenclature and origin (i.e., native vs. non-native) determination for this study followed the USDA PLANTS Database (USDA NRCS, 2017) and Mincemoyer (2013).

## 2.3. Data analyses

We used generalized linear mixed-effects models (PROC GLIMMIX in SAS 9.4; SAS Institute Inc. 2016) to compare understory vegetation measurements among treatments and across years. Cover and species richness for each of the five growth form × origin groups were treated as response variables in separate models. For each model, we specified the error distribution that provided the best fit (lognormal for cover variables to account for positive skewness and either a negative binomial or Poisson for species richness variables given count data). Treatment (including CO in 2007 and 2015), measurement year (seven years including pre-treatment), and their interaction were included in models as fixed factors, with the latter testing for variation in treatment effects over time. In addition, experimental unit and experimental unit within year were included as random factors to account for covariance in responses therein, and responses per plot and year were treated as repeated measures. When the treatment × year interaction was statistically significant ( $\alpha = 0.05$ ), we used post-hoc comparisons to test for differences among treatments in each measurement year. P-values for

post-hoc tests were adjusted by the simulation method (Hsu and Nelson, 1998), and a less conservative cutoff of  $\alpha = 0.10$  was used for interpretation of pairwise differences to better identify potential treatment-level differences.

For exploratory analysis, understory cover response variables defined by growth form  $\times$  origin were further split by life form into perennial vs. annual (including biennial) species. Note that this was not done for native shrubs given that all species were perennials. For forb and graminoid groups, perennial species comprised the majority of cover in most cases across treatments and years. Similarly, perennial cover was highly correlated with total cover for native forbs (spearman  $r = 0.95$ ,  $P < 0.001$ ), non-native forbs (spearman  $r = 0.93$ ,  $P < 0.001$ ), and native graminoids (spearman  $r = 0.99$ ,  $P < 0.001$ ), and moderately so for non-native graminoids (spearman  $r = 0.76$ ,  $P < 0.001$ ). In addition, cover of annual species was low in most cases (see Results). Hence, we did not present statistical analyses for cover groups split by growth form, but do include a qualitative description of patterns for annual species based on means by treatment and year. For species richness measures, counts by growth form and origin were generally too low to allow further splitting by life form, and these groups were not analyzed further.

We also examined the fine-scale relationship between each understory response variable and basal area to examine the potential influence of overstory conditions on vegetation outcomes in the final measurement year (2015). We used the error distributions specified above to construct a model for each response variable and included experimental unit as a random factor and basal area as a fixed effect (covariate). We also included treatment (including CO) as a fixed factor to account for its potential influence on responses and to test whether differences among treatments were apparent even when controlling for variation in overstory conditions. Finally, we included the basal area  $\times$  treatment interaction to test whether relationships between understory and overstory conditions varied by treatment.

Constrained correspondence analysis (also known as canonical correspondence analysis; CCA) (ter Braak, 1987) was used to investigate the effects of treatment, measurement year, and their interaction on the understory vegetation community. This analysis is essentially a hybrid of an ordination method (correspondence analysis) and regression analysis, providing a useful way to test the effects of explanatory variables on biological communities (ter Braak and Verdonschot, 1995). The basic principle of CCA is to identify the linear combination of constraints (e.g., environmental variables or treatments in this study) associated with the maximum dispersion of species scores (ter Braak, 1987), as represented by cover in our analysis. We used a permutation test to assess differences in understory vegetation composition by the specified constraints. The permutation test compared the observed constraints' inertia (weighted variance) with randomly permuted and refitted constraints' inertia across 1000 iterations (Oksanen et al., 2017). The CCA and permutation test were conducted with the vegan package (Oksanen et al., 2017) in R (ver. 3.5.0; R Core Team, 2018).

Finally, we used an indicator species analysis to identify key species responses to treatments (De Cáceres and Legendre, 2009; De Cáceres et al., 2010). Indicator species analysis uses an indicator value index, which is maximized when a species is found exclusively or abundantly in a specific treatment (Dufrene and Legendre, 1997). We conducted this analysis using the explanatory terms that were identified as statistically significant ( $\alpha = 0.05$ ) in the CCA permutation tests, while frequency values were used as the response (Livingston et al., 2016). Data were also pooled by treatment to test the effects of time, and then pooled by time to test the effects of treatment on indicator species. This analysis was run with 1000 permutations using the indicpecies package (De Cáceres and Jansen, 2016) in R (ver. 3.5.0; R Core Team, 2018). For both CCA and indicator species analyses, we included only those understory species with mean relative cover (proportion of total plot cover at time of measurement)  $>5\%$ .

### 3. Results

A total of 183 vascular plant species were identified throughout the field surveys from 1991 to 2015, consisting of 5 tree, 18 shrub, 124 forb, and 36 graminoid species (see Lutes et al. 2020 for full species list and archived data). Among them, 37 non-native species were observed: 10 graminoids and 27 forbs. In the final sampling year (23 years after shelterwood harvest and burning treatments), dominant native species included the native shrub *Arctostaphylos uva-ursi*, the native forb *Lupinus sericeus*, and the native graminoid *Calamagrostis rubescens* (Table 1). For non-native species, dominant forbs included *Centaurea stoebe* and *Hieracium caespitosum*, and dominant graminoids were *Apera interrupta* and *Bromus tectorum* (Table 1). One hundred fourteen of the 183 species had  $>5\%$  mean relative plot cover in at least one post-treatment measurement year.

#### 3.1. Understory vegetation cover

For both native and non-native forbs, cover varied significantly among years ( $P < 0.001$ , Table 2), generally peaking 3–5 years after restoration treatments were initiated and decreasing thereafter (Fig. 1a, b). Cover of these groups did not differ significantly among treatments prior to cutting and burning, but marked differences emerged in subsequent years, particularly in years of peak cover (treatment  $\times$  year:  $P < 0.008$ ; Table 2; Fig. 1a). For native forbs, differences among treatments were greatest in post-treatment year 3, when mean cover was significantly higher in DB compared to NB units, with intermediate levels in WB units. However, even in post-treatment years 15 and 23, when mean cover of native forbs was roughly half that recorded in peak years, treatment effects were still apparent. In these final sampling years, native forb cover was significantly higher in treated (DB, WB, and NB) relative to CO units (Table 3). These patterns in native forb cover were driven by perennial species, which comprised the majority of cover across treatments and years (mean = 90% of total native forb cover). Native annual forb cover showed a similar trajectory, with a particularly sharp peak in DB units in post-treatment year 3 (Fig. 2a).

Patterns were similar for non-native forb cover, although differences among treatments were apparent sooner and were also more

**Table 1**

Major (top 3) understory species in the Lick Creek Demonstration-Research Forest, 23 years after shelterwood-with-reserves harvesting and subsequent burning treatments, as measured by mean cover in groups defined by life form ( $P =$  perennial,  $A =$  annual) and species origin. Also given is relative cover as a proportion of mean total cover per group.

Species name	Life form	Mean cover (%)	Relative cover (%)
Native forb			
<i>Lupinus sericeus</i> Pursh	P	3.4	25.3
<i>Apocynum androsaemifolium</i> L.	P	2.1	15.4
<i>Arnica cordifolia</i> Hook.	P	1.5	11.2
Native graminoid			
<i>Calamagrostis rubescens</i> Buckley	P	6.4	47.0
<i>Carex geyeri</i> Boott	P	5.3	38.9
<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve	P	0.7	7.3
ssp. <i>spicata</i>			
Native shrub			
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	P	5.8	42.1
<i>Symphoricarpos albus</i> (L.) S.F. Blake	P	2.4	17.3
<i>Berberis repens</i> (Lindl.) G. Don	P	1.7	12.7
Non-native forb			
<i>Centaurea stoebe</i> L. ssp. <i>micranthos</i> (Gugler) Hayek	P	1.0	62.2
<i>Hieracium caespitosum</i> Dumort.	P	0.4	21.2
<i>Medicago lupulina</i> L.	A/P	0.1	6.4
Non-native graminoid			
<i>Apera interrupta</i> (L.) P. Beauv.	A	0.3	62.1
<i>Bromus tectorum</i> L.	A	0.2	29.3
<i>Dactylis glomerata</i> L.	P	<0.1	3.4



**Table 2**

Results of generalized linear mixed model analysis testing for differences among restoration treatments over time for understory vegetation cover and species richness variables measured in the Lick Creek Demonstration-Research Forest. Bold fonts represent significant test results ( $\alpha = 0.05$ ). Abbreviations of Num df and Den df represent the degrees of freedom for numerator and denominator, respectively.

Model	Variance Source	Num df	Den df	F Value	P-value
<b>Cover (%)</b>					
Native Forb	Treatment (T)	3	8	6.46	<b>0.016</b>
	Year (Y)	6	38	33.75	<b>&lt;0.001</b>
	T × Y	13	38	2.72	<b>0.008</b>
Native Graminoid	Treatment (T)	3	8	0.24	0.868
	Year (Y)	6	38	20.83	<b>&lt;0.001</b>
	T × Y	13	38	1.01	0.459
Native Shrub	Treatment (T)	3	8	0.59	0.636
	Year (Y)	6	38	18.41	<b>&lt;0.001</b>
	T × Y	13	38	0.76	0.693
Non-native Forb	Treatment (T)	3	8	20.99	<b>&lt;0.001</b>
	Year (Y)	6	38	77.10	<b>&lt;0.001</b>
	T × Y	13	38	3.08	<b>0.003</b>
Non-native Graminoid	Treatment (T)	3	8	7.20	<b>0.012</b>
	Year (Y)	6	38	6.11	<b>&lt;0.001</b>
	T × Y	13	38	1.97	0.053
<b>Richness</b>					
Native Forb	Treatment (T)	3	8	5.91	<b>0.020</b>
	Year (Y)	6	38	13.79	<b>&lt;0.001</b>
	T × Y	13	38	0.86	0.599
Native Graminoid <sup>†</sup>	Treatment (T)	3	8	1.13	0.392
	Year (Y)	6	38	18.48	<b>&lt;0.001</b>
	T × Y	13	38	1.48	0.170
Native Shrub <sup>†</sup>	Treatment (T)	3	8	0.32	0.760
	Year (Y)	6	38	18.61	<b>0.021</b>
	T × Y	13	38	2.01	0.932
Non-native Forb	Treatment (T)	3	8	3.92	0.054
	Year (Y)	6	38	3.64	<b>0.006</b>
	T × Y	13	38	0.13	1.000
Non-native Graminoid <sup>†</sup>	Treatment (T)	3	8	0.07	0.977
	Year (Y)	6	38	5.80	<b>&lt;0.001</b>
	T × Y	13	38	1.66	0.113

<sup>†</sup> Poisson error distribution was used for these response variables.

pronounced despite the fact that pre-treatment levels of cover were very low for this group (<2% mean cover) compared to native forbs (>9% mean cover; Fig. 1d). As soon as post-treatment year 2, non-native forb cover was significantly higher in DB vs. NB units, with intermediate levels in WB units (Table 3). These differences peaked in post-treatment year 3, when mean non-native forb cover was 4 to 5-fold higher in DB and WB (i.e., burned) vs. NB (i.e., unburned) units, and were still large in post-treatment year 5, when the difference in DB and WB vs. NB units was 2 to 3-fold. The response of non-native forbs to cutting and burning was so strong that mean cover of this group in WB and especially DB units approached levels observed for native forbs during post-treatment years 3–5. This pattern of treatment differences persisted through the final years of sampling, although non-native forb cover diminished substantially and differences among treatments were much smaller. Specifically, in post-treatment years 15 and 23, non-native forb cover remained significantly higher in DB and WB units relative to CO units, with NB units falling at intermediate levels and clustering with CO units (Table 3). As seen for native forbs, the overall pattern for non-native forbs was driven by the response of perennials, which comprised the majority of cover (mean = 81% of total native forb cover) across treatments and years. Non-native annuals followed a parallel pattern, but cover of this group showed a steeper peak centered on post-treatment year 3, particularly in the burned units (Fig. 2b).

As seen for forb groups, both native and non-native graminoid cover varied significantly among years ( $P < 0.001$ , Table 2), peaking 3–5 years after treatment following an initial decline from pre-treatment levels

(Fig. 1b). Native graminoid cover did not differ among treatments in any year (treatment × year:  $P = 0.46$ ). These species were overwhelmingly dominated by perennials, which comprised > 98% of the cover for this group across treatment types and years. Annual grasses were represented by just one species (*Vulpia octiflora* (Walter) Rydb. var. *glauca* (Nutt.) Fernald), which showed a sharp peak in years 3–5 in the burned units.

For non-native graminoid cover, differences among treatments emerged in the post-treatment period (treatment × year:  $P = 0.05$ ; Table 2). The pattern for non-native graminoid cover seen in the early post-treatment years was driven by non-native perennials, which constituted the majority of cover (mean = 82% of total non-native graminoid cover) during this period, and peaked in post-treatment year 4 in a similar manner across treatments. Significant differences were not evident until post-treatment years 15 and 23, when non-native graminoid cover was higher in DB and WB units compared to NB (in year 15) and CO units (in both years 15 and 23; Table 3). These differences among treatments were driven by non-native annual graminoids, which were the dominant group in the later post-treatment years, particularly in the burned units (Fig. 2d). Even though mean non-native graminoid cover was >12-fold higher in DB and WB units relative to NB and CO units in these years, mean levels in all treatments were low for this group (<3%) relative to native graminoids (>9%).

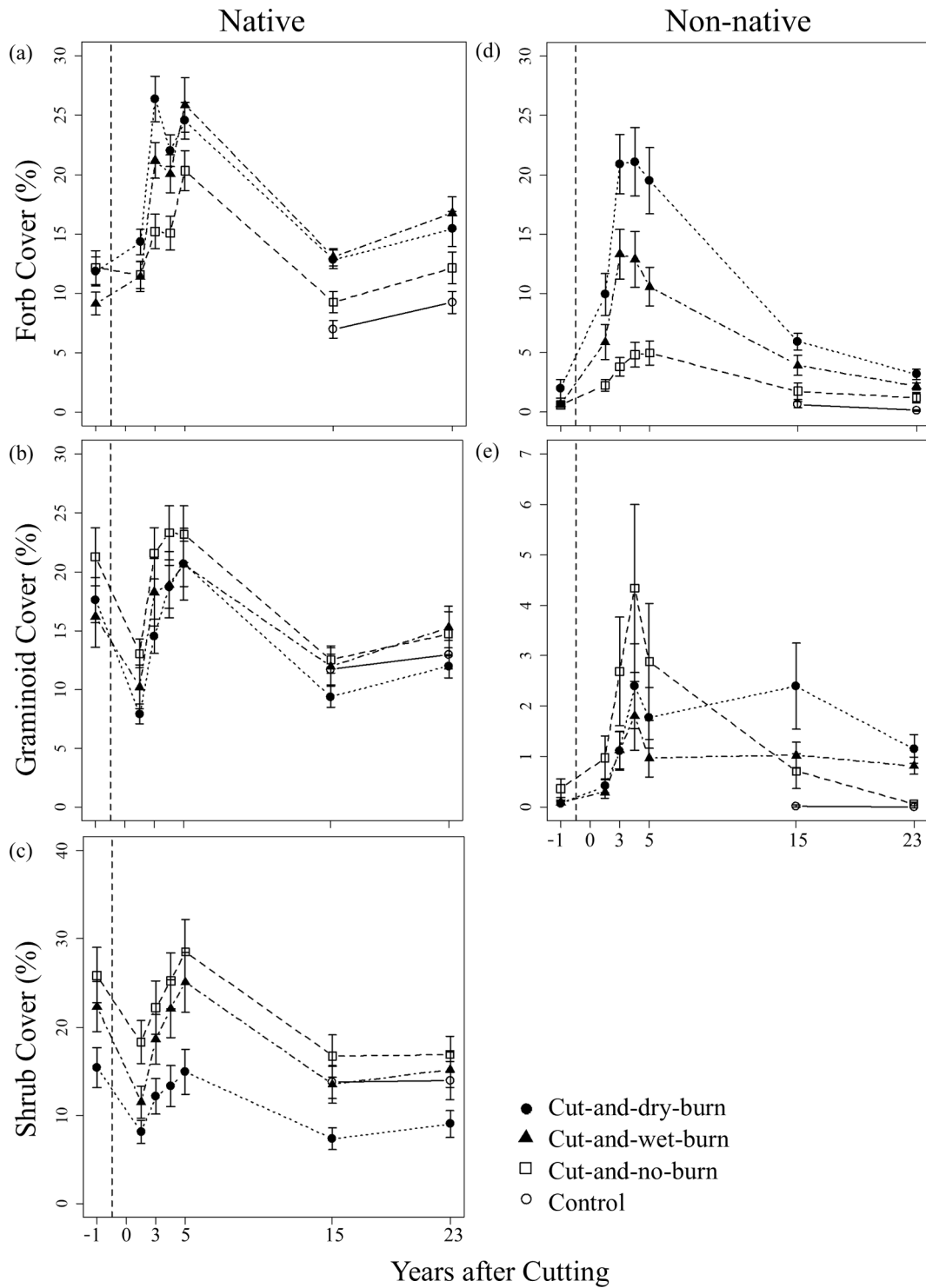
Native shrub cover followed a similar temporal pattern as seen for native graminoids, with significant variation among years and a brief post-treatment decline before reaching peak levels 5 years after treatment and maintaining modest levels thereafter ( $P < 0.001$ , Table 2, Fig. 1c). However, as seen for native graminoids, native shrub cover did not differ significantly among treatments in any year (treatment × year:  $P = 0.69$ ; Table 3).

### 3.2. Understory species richness

Native forb species richness was more than three times that of non-native forbs, although temporal patterns were similar between groups (Fig. 3). For both native and non-native forbs, richness differed significantly among years ( $P < 0.01$ ), with a peak in post-treatment years 3–5, as seen for cover, though temporal variation was relatively low (Table 2, Fig. 3a). Richness of both forb groups differed among treatments overall ( $P \leq 0.02$ ), again with a tendency for higher levels in burned (DB and WB) vs. unburned (NB) and untreated (CO) units (Fig. 3a); however, differences among treatments did not vary significantly among sampling years (treatment × year:  $P > 0.5$ ). For graminoid groups and for shrubs, species richness varied significantly among years ( $P < 0.01$ ), although changes were minimal and did not differ among treatments ( $P > 0.1$ , Table 2, Fig. 3b,c).

### 3.3. Effects of overstory trees

In the final measurement year, 23 years after treatment, overstory basal area varied from 5.1 m<sup>2</sup> ha<sup>-1</sup> to 54.7 m<sup>2</sup> ha<sup>-1</sup> and was negatively associated with native and non-native forb cover and richness, and native shrub cover ( $P < 0.04$ , Table 4). Non-native graminoid cover had a similar relationship with overstory basal area ( $P = 0.083$ ), and native shrub richness varied positively with overstory basal area ( $P = 0.05$ , Table 4). In most of these cases, understory responses did not differ significantly among treatments when overstory basal area was accounted for (Table 4). However, non-native forb cover differed significantly ( $P < 0.001$ ) among treatments even when the effect of overstory conditions was controlled for, with significantly higher levels in burned (DB and WB) compared to unburned (NB) treatments ( $P < 0.005$ ) and in treated (DB, WB, and NB) compared to untreated (CO) units ( $P < 0.002$ ). Non-native graminoid cover also differed among treatments when overstory basal area was accounted for, following a similar pattern as seen for non-native forb cover (DB and WB vs. NB,  $P \leq 0.1$ ; DB and WB vs. CO,  $P < 0.08$ ; NB vs. CO,  $P > 0.99$ ). Relationships between



**Fig. 1.** Changes in native and non-native plant cover by restoration treatment over time. Cover was calculated by plant class: forbs (panels a and d), graminoids (panels b and e), and shrubs (panel c). Note that no non-native shrubs were recorded. Means ( $\pm 1$  standard error) are represented prior to treatment (1 year before harvest; labeled as -1), and in post-treatment years 2–5, 15, and 23, respectively.

understory response variables and overstory basal area did not differ significantly among treatments in any case (i.e., overstory  $\times$  treatment:  $P > 0.07$ , Table 4).

### 3.4. Understory species composition responses to treatment

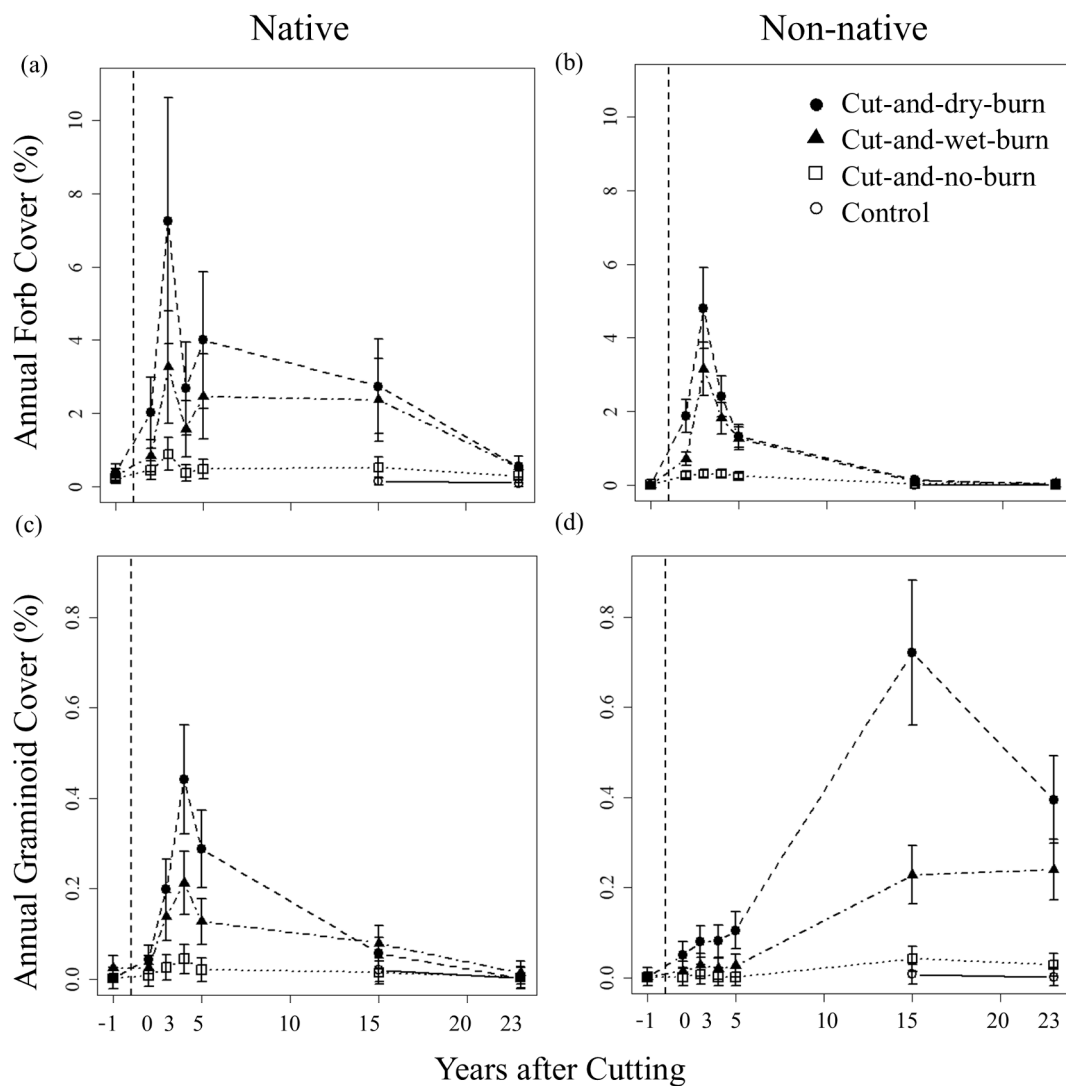
Initial species composition (i.e., pre-treatment, -1) differed significantly among treatments (Table 5), although differences were relatively

small in CCA space (Fig. 4). As expected, composition shifted further following treatment in burned (DB and WB units; average distance in the CCA projection = 1.85; Fig. 4) than in unburned (NB) units (distance = 0.62) 2 years post-treatment, signifying that burned units had similar understory vegetation composition shortly after treatment. The treatments differed significantly from each other through post-treatment year 15. (Table 5). Twenty-three years after harvesting, species compositions of all treatments were represented in the lower left quadrant of

**Table 3**

Post-hoc comparisons of understory vegetation cover variables by restoration treatment and sampling year, as assessed via generalized linear mixed models. Letters indicate significant differences among treatments within a year ( $\alpha = 0.10$ ). Blank cells represent non-significant test results, and dashes indicate that no test was conducted due to a lack of data. Native graminoid and shrub results were excluded because there were no significant differences. Treatments were DB = cut-and-dry-burn, WB = cut-and-wet-burn, NB = cut-and-no-burn, and CO = control.

Year	Native				Non-native								
	Forb				Forb				Graminoid				
	DB	WB	NB	CO	DB	WB	NB	CO	DB	WB	NB	CO	
Cover (%)													
Pre-treatment				–				–					–
2-yr post-treatment				–	a	ab	b	–					–
3-yr post-treatment	a	ab	b	–	a	a	b	–					–
4-yr post-treatment				–	a	a	b	–					–
5-yr post-treatment				–	a	ab	b	–					–
15-yr post-treatment	a	a	a	b	a	a	b	b	a	a	ab	b	
23-yr post-treatment	a	a	a	b	a	a	ab	b	a	a	ab	b	

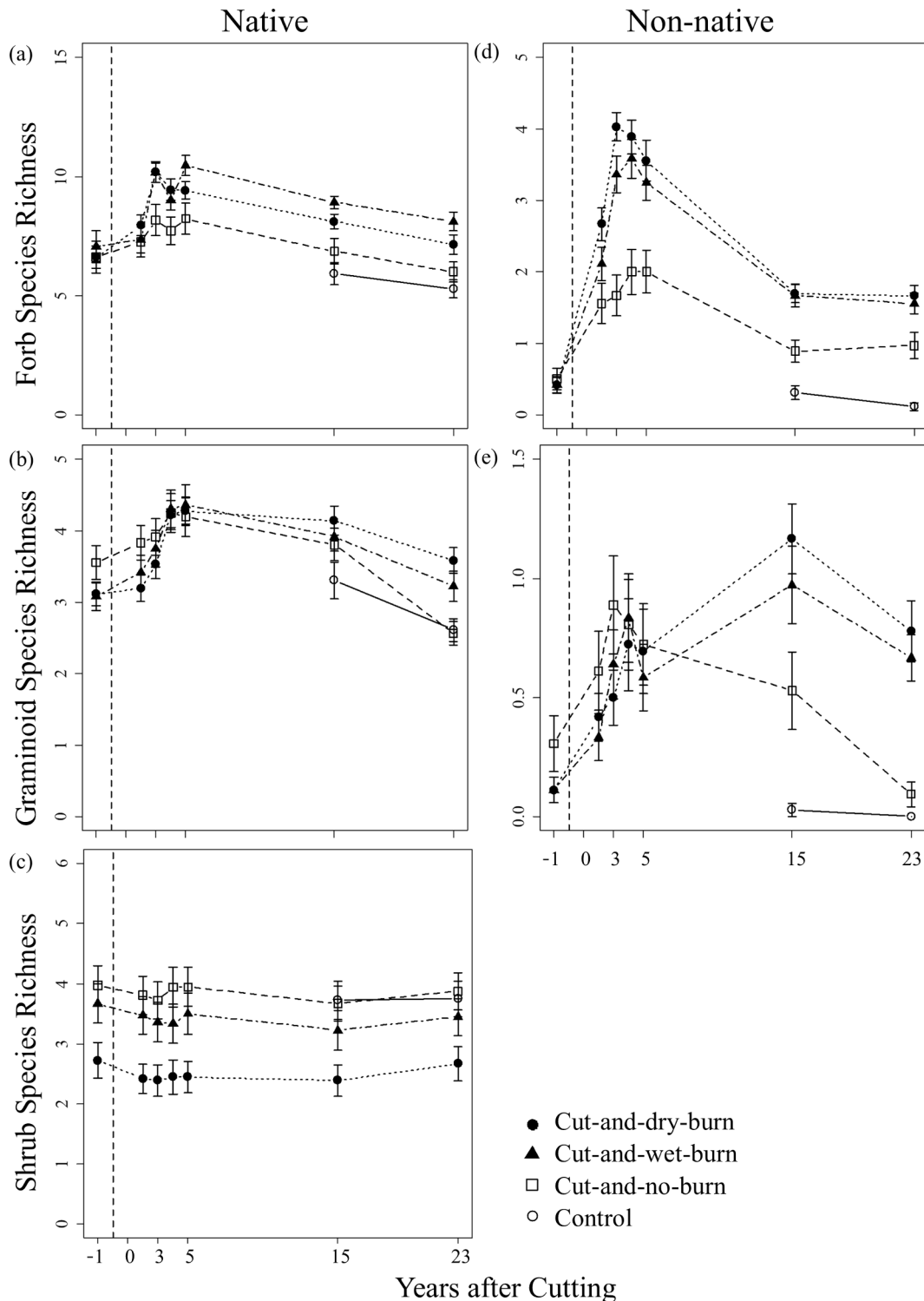


**Fig. 2.** Changes in (a) native annual forb, (b) non-native annual forb, (c) native annual graminoid, and (d) non-native annual graminoid cover by restoration treatment over time. Note that all shrubs were perennial so excluded here. Means ( $\pm 1$  standard error) are represented prior to treatment (1 year before harvest; labeled as -1), and in post-treatment years 2–5, 15, and 23, respectively.

the plot. At this last measurement, DB treatment composition was different than WB, NB, and CO; WB was still different than CO, but no longer distinguishable from NB (Table 5). Vegetation composition was not different between NB and CO units in post-treatment years 15 and 23. Projection distances from pre-treatment to final measurement were

larger as the intensity of disturbance increased (3.49, 3.40, and 2.14 for DB, WB, and NB, respectively).

Our analysis identified 29 unique indicator species over the whole 23-year measurement period (Table 6). Eighteen indicator species were forbs (13 perennial, 5 biennial or annual), 5 of which were non-natives



**Fig. 3.** Changes in native and non-native plant species richness by restoration treatment over time. Richness was tallied by plant class: forbs (panels a and d), graminoids (panels b and e), and shrubs (panel c). Note that no non-native shrubs were recorded. Means ( $\pm 1$  standard error) are represented prior to treatment (1 year before harvest; labeled as -1), and in post-treatment years 2–5, 15, and 23, respectively.

(3 perennials, 2 biennials). Non-native species were more frequently identified as indicator species for the DB treatment than other treatments, as were short-lived (biennial or annual) species, with both groups consisting primarily of forbs. The importance of forb, non-native, and short-lived species in distinguishing treatments paralleled results observed for cover (Figs. 1 and 2, Tables 2 and 3). Overall, the DB treatment had the most indicator species (15 species after harvesting)

across years, emphasizing this treatment’s compositional uniqueness.

#### 4. Discussion

##### 4.1. Understory vegetation response

Prior work at Lick Creek demonstrated that all the forest restoration



**Table 4**

Results of generalized linear mixed model analysis testing for relationships between understory responses and overstory basal area while accounting for treatment. Significant tests ( $\alpha = 0.05$ ) are highlighted in bold. Degrees of freedom (numerator and denominator) for overstory basal area, treatment, and their interaction were 1 and 124, 3 and 8, and 3 and 124, respectively.

	Overstory			Treatment		Overstory $\times$ Treatment	
	$\beta$ (SE) <sup>†</sup>	F	P	F	P	F	P
<b>Cover</b>							
Native forb	-0.042 (0.020)	8.20	<b>0.005</b>	1.20	0.370	0.70	0.554
Native graminoid	0.002 (0.022)	<0.01	0.947	0.95	0.463	0.94	0.421
Native shrub	-0.029 (0.041)	13.98	<b>&lt;0.001</b>	1.08	0.413	2.37	0.074
Non-native forb	-0.079 (0.034)	8.85	<b>0.004</b>	6.01	<b>0.019</b>	0.84	0.475
Non-native graminoid	-0.042 (0.034)	3.05	0.083	3.32	0.078	0.88	0.456
<b>Richness</b>							
Native forb	-0.026 (0.014)	4.57	<b>0.035</b>	0.41	0.752	1.15	0.333
Native graminoid	-0.009 (0.022)	0.28	0.601	0.02	0.995	0.15	0.930
Native shrub	0.0004 (0.018)	3.90	<b>0.050</b>	0.62	0.624	1.24	0.298
Non-native forb	-0.042 (0.036)	5.67	<b>0.019</b>	0.50	0.692	0.80	0.497
Non-native graminoid	-0.278 (0.151)	<0.01	0.998	0.51	0.685	<0.01	0.998

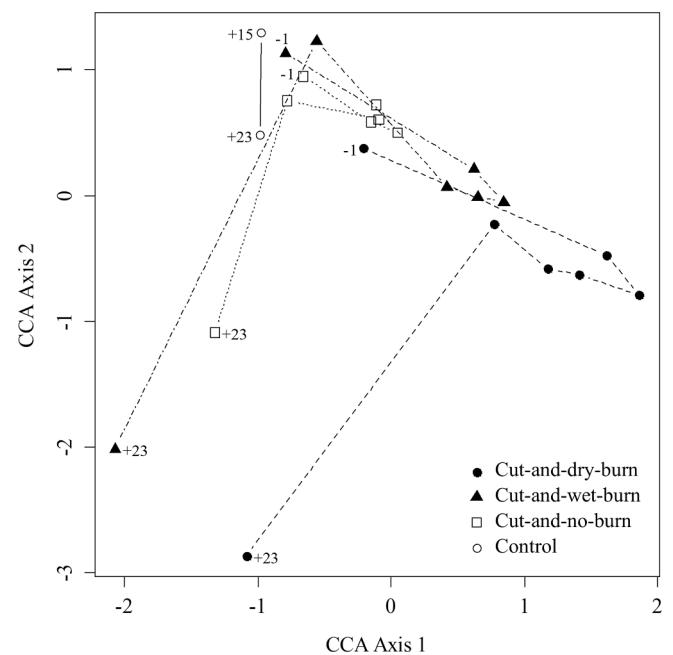
<sup>†</sup> Parameter estimates are given on the natural log scale in accordance with the specified error distribution.

**Table 5**

Post-hoc comparisons of understory vegetation species composition by restoration treatment and sampling year, as assessed via constrained correspondence analysis permutation tests. Letters indicate significant differences among treatments within a year ( $\alpha = 0.10$ ). Treatments were DB = cut-and-dry-burn, WB = cut-and-wet-burn, NB = cut-and-no-burn, and CO = control.

Year	Treatment			
	DB	WB	NB	CO
Pre-treatment	a	b	c	-
+2 year	a	b	b	-
+3 year	a	b	c	-
+4 year	a	b	c	-
+5 year	a	b	c	-
+15 year	a	b	c	c
+23 year	a	b	bc	c

treatments we evaluated can effectively restore overstory tree composition, reduce tree densities, and decrease canopy fuel loads in the short-term (<5 years; Smith and Arno, 1999), but the more intensive treatments involving both cutting and burning are most effective at restoring pine-dominated, low overstory densities and canopy fuels over both short and longer time frames (Clyatt et al., 2017; Hood et al., 2020). That said, more intensive treatments cause greater disturbance which can negatively impact understory vegetation and facilitate non-native species establishment (e.g., Davis et al., 2000; Collins et al., 2007), at least in the first few years following treatment. Recent studies have just begun to demonstrate how these effects play out over long time periods (Nelson et al., 2008; Kerns and Day, 2018; Rossman et al., 2018; Croteau et al., 2020; Korb et al., 2020). In conducting a long-term (23-year) experimental study of understory species responses to these forest restoration treatments, we found that native and non-native plant cover increased strongly 3–5 years after overstory tree removal, particularly when combined with prescribed burning, but responses settled substantially for most functional groups by year 23 (Fig. 1). Nonetheless, non-native species generally responded much more strongly to treatments than did natives, resulting in greater short-term increases that were closely linked to treatment intensity. For non-native species in particular, differences among treatments could not be explained by variation in overstory conditions, suggesting that higher levels of disturbance associated with more intensive treatments (i.e., burning) favored these taxa. While replication was low and experimental units were close together in this study, these dry ponderosa pine-Douglas-fir systems are rather homogeneous, and the study sites are likely well representative of system responses. As we discuss below, our findings provide valuable insights regarding how these forest restoration treatments affect understory plant communities and their susceptibility to



**Fig. 4.** Temporal shift of understory vegetation species composition by type of restoration treatment as assessed through constrained correspondence analysis (CCA). Points represent the mean of site scores by restoration treatment and measurement year. Measured composition is shown prior to treatment (1 year before harvest; represented in the upper left to center region; labeled as -1), and in post-treatment years 2–5, 15 (transitioned downward and to the right; labeled as +15 for control units only), and 23 (represented in the lower left; labeled as +23), respectively.

invasion for improved forest management.

Overall, understory species responded to reductions in overstory tree densities as predicted from successional theory (Connell, 1978), with cover of most functional groups peaking about 3–5 years following treatment (following an immediate but brief decline in abundance of native grasses and shrubs), and then declining to levels generally comparable to pre-treatment levels as mature and regenerating trees reoccupied space. Species richness generally followed a similar pattern. Notably, cover responses tended to be more exaggerated in the more intensive treatments involving both cutting and burning, suggesting that the level of disturbance was driving these responses. While the inclusion of fire may have contributed unique factors like temporary reductions in competition and increases in nutrient availability (DeLuca and Zouhar, 2000; Gundale et al., 2005; DeLuca and Sala, 2006; Moore et al., 2006),

**Table 6**

Indicator species analysis by sampling year and restoration treatment. Indicator values were according to De Cáceres and Legendre (2009) and De Cáceres (2010). Note that control units were measured only in 2007 (15 years post-treatment) and 2015 (23 years post-treatment). Indicator species is labeled n.s. where no species was identified as significant. Treatments were DB = cut-and-dry-burn, WB = cut-and-wet-burn, NB = cut-and-no-burn, and CO = control.

Treatment/time	Indicator Species	Origin	Growth form	Life form	Specificity	Fidelity	Indicator Value
Pre-treatment							
DB	<i>Carex geyeri</i> Boott	Native	Graminoid	Perennial	0.09	0.75	0.26
WB	<i>Vaccinium cespitosum</i> Michx.	Native	Shrub	Perennial	0.22	0.20	0.21
	<i>Vaccinium membranaceum</i> Douglas ex Torr.	Native	Shrub	Perennial	0.75	0.06	0.21
NB	n.s.						
2-yr post-treatment							
	<i>Silene menziesii</i> Hook.	Native	Forb	Perennial	0.51	0.14	0.27
DB	<i>Claytonia perfoliata</i> Donn ex Willd. ssp. <i>perfoliata</i>	Native	Forb	Annual	0.40	0.08	0.18
WB	n.s.						
	<i>Trisetum spicatum</i> (L.) K. Richt.	Native	Graminoid	Perennial	0.42	0.09	0.19
NB							
3-yr post-treatment							
	<i>Epilobium brachycarpum</i> C. Presl	Native	Forb	Annual	0.33	0.42	0.37
DB	<i>Verbascum thapsus</i> L.	Non-native	Forb	Biennial	0.20	0.67	0.37
	<i>Rumex acetosella</i> L.	Non-native	Forb	Perennial	0.20	0.53	0.33
	<i>Coryza canadensis</i> (L.) Cronquist	Non-native	Forb	Annual	0.79	0.11	0.30
	<i>Vulpia octoflora</i> (Walter) Rydb. var. <i>glauca</i> (Nutt.) Fernald	native	Graminoid	Annual	0.25	0.14	0.19
WB	<i>Trisetum</i> spp.	Native	Graminoid	Perennial	0.55	0.08	0.21
NB	<i>Agrostis</i> spp.	Native	Graminoid	Perennial	0.21	0.17	0.19
		Native					
		Non-native					
4-yr post-treatment							
	<i>Apocynum androsaemifolium</i> L.	Native	Forb	Perennial	0.08	0.69	0.22
DB	<i>Carex rossii</i> Boott	Native	Graminoid	Perennial	0.13	0.31	0.20
WB	<i>Cirsium vulgare</i> (Savi) Ten.	Non-native	Forb	Biennial	0.14	0.33	0.22
NB	<i>Poa pratensis</i> L.	Non-native	Graminoid	Perennial	0.38	0.17	0.25
		Non-native					
5-yr post-treatment							
	<i>Centaurea stoebe</i> L. ssp. <i>micranthos</i> (Gugler) Hayek	Non-native	Forb	Perennial	0.13	0.67	0.30
DB	<i>Pseudognaphalium canescens</i> (DC.) W.A. Weber ssp. <i>microcephalum</i> (Nutt.) Kartesz	Non-native	Forb	Perennial	0.62	0.08	0.23
		Native					
WB	<i>Antennaria microphylla</i> Rydb.		Forb	Perennial	0.16	0.19	0.18
	<i>Hieracium</i> spp.	Native	Forb	Perennial	0.31	0.14	0.21
NB	<i>Carex concinna</i> R. Br.	Native	Graminoid	Perennial	0.22	0.19	0.21
	<i>Rosa</i> spp.	Native	Shrub	Perennial	0.12	0.25	0.18
		Native					
15-yr post-treatment							
	<i>Lupinus</i> spp.	Native	Forb	Perennial	0.16	0.28	0.21
DB	<i>Carex</i> spp.	Native	Graminoid	Perennial	0.74	0.15	0.33
WB	<i>Galium boreale</i> L.	Native	Forb	Perennial	0.46	0.06	0.17
NB	<i>Vaccinium</i> spp.	Native	Shrub	Perennial	0.95	0.29	0.53
CO							
23-yr post-treatment							
	<i>Hieracium caespitosum</i> Dumort.	Non-native	Forb	Perennial	0.88	0.11	0.31
DB	<i>Rosa gymnocarpa</i> Nutt.	Non-native	Shrub	Perennial	0.47	0.11	0.23
	<i>Lupinus sericeus</i> Pursh	Native	Forb	Perennial	0.40	0.61	0.49
WB	<i>Solidago simplex</i> Kunth	Native	Forb	Perennial	1.00	0.06	0.24
	<i>Lupinus lepidus</i> Douglas ex Lindl.	Native	Forb	Perennial	0.17	0.23	0.20
NB	<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem.	Native	Shrub	Perennial	0.29	0.10	0.17
	<i>Arnica cordifolia</i> Hook.	Native	Forb	Perennial	0.25	0.42	0.32
CO		Native					

the lack of a fire-only treatment precluded us from isolating such effects. Nonetheless, it appeared that the combined treatments (cut-and-dry-burn and cut-and-wet-burn vs. cut-and-no-burn), and especially the most intense of these (cut-and-dry-burn), tended to amplify understory responses over cutting alone.

Of all growth forms that we studied, forbs, particularly perennial species, appeared to respond the most to restoration. Treatments that included prescribed fire especially benefitted cover and richness of this group (Gundale et al., 2005; Wayman and North, 2007; Lyon and Stickney, 1976), perhaps because of the high initial prevalence of this group. Annual forbs were much less abundant but also showed strong short-term responses that scaled with treatment intensity. On the other hand, graminoid and shrub richness, consisting almost entirely of perennial taxa, was low (i.e., at or below five species each) and relatively

stable, varying by less than two species over the entire measurement period. Similarly, cover of these native groups was less sensitive to treatments. Overall, these results corroborate short-term responses to restoration treatments documented in other dry coniferous forests (e.g., Dodson et al., 2007, 2008; Metlen and Fiedler, 2006; Moore et al., 2006) and indicate that forbs play a critical role in understory revegetation dynamics following treatment (Laughlin et al., 2008).

Non-native species responses directly paralleled those of the natives, but non-natives exhibited much stronger short-term increases, particularly in the higher intensity treatments involving burning. As with native species, these increases in non-native taxa were primarily driven by perennial forbs, especially the tap-rooted *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek. Short-lived forbs and perennial rhizomatous grasses also played a role in the early post-treatment period, while

annual grasses became more important in the later years (Table 6). The fact that adding the covariate for overstory basal area to models explained native but not non-native responses in post-treatment year 23 (i.e., differences among treatments were no longer evident) suggests that the non-native taxa were more effective at taking advantage of disturbance/resource pulses linked to the treatments than were the natives (Davis et al., 2000; Jauni et al., 2015; Pearson et al., 2018). Overall, understory responses in our dry forest system show a high level of resiliency to restoration treatments (as in Dodson et al., 2008; Metlen and Fiedler, 2006). However, the stronger responses of non-native species, particularly to higher-intensity treatments, indicate a degree of susceptibility to invasion that should be considered when applying forest restoration treatments, particularly if re-entry maintenance treatments occur on short time scales.

Our CCA and permutation tests indicated that treatments did not lead to clearly distinct communities through time. Rather, plot-scale species composition remained quite heterogeneous over time, and no species exceeded 10% of understory cover in any treatment. Thus, treatment distinctiveness was attributed to different low-coverage species assemblages rather than high-cover dominance by select species. Because these treatments were implemented at the same time and at nearby sites, differences in species composition were presumably driven by treatment and slight differences in initial (pre-existing) species composition (Fulé et al., 2005; Wayman and North, 2007).

Interestingly, we observed parallel compositional shifts in both burning treatments on the CCA projection (Fig. 4), implying similar species composition changes. Despite the different moisture conditions in the treatment burning windows, our cut-and-wet-burn and cut-and-dry-burn treatments were only implemented two weeks apart, therefore any treatment differences are more attributable to differences in burn consumption than vegetation phenology. Duff consumption (from depth measurements) was 2.2 times greater in the cut-and-dry-burn than cut-and-wet-burn, demonstrating the greater prescribed fire intensity and impact in the former treatment (Harrington, 1999). Assuming the distance between year 15 and 23 for control units as a measure of natural variability, cut-and-no-burn units exhibited a similar level (i.e., distance between points) of compositional changes as this baseline, whereas burning treatments had more drastic shifts at the same period (Fig. 4; Table 5). Therefore, final distances (i.e., year 23) from the control on the CCA plane likely reflect the enduring effects of disturbance intensity (Fig. 4).

Prevalence of the indicator species across treatments demonstrates species' tolerance and competitiveness following the disturbance (White et al., 1990). Temporal transition of indicator species should theoretically follow general successional trends, at first dominated by early-seral opportunists but followed by late-successional species (Crawford et al., 2001). Immediately after the treatments, we found distinctive fire-stimulated, re-sprouting species of perennial forbs in the burned units (e.g., *Silene menziesii* Hook. and *Apocynum androsaemifolium* L.). In contrast, if they could not survive burning, non-sprouting plant species (i.e., *Trisetum spicatum* (L.) K. Richt.) were exclusively observed in the cut-and-no-burn treatment (Lyon and Stickney, 1976; Stickney and Campbell, 2000; Dodson et al., 2007). Shortly thereafter (i.e., 3 years post-treatment), treatments were distinguished by rapid-spreading colonizers such as *Epilobium brachycarpum* C. Presl and non-native invasive species presumably seeded in and established from unburned sites. By 15 and 23 years post-treatment, shade-tolerant plant species characterized the controls while shade-intolerant *Lupinus* spp. helped to distinguish the treated units; only the cut-and-dry-burn treatment was still distinguished by a non-native species. Overall, the results indicated that the re-sprouting plant species can survive and are resilient to the low-intensity fires of our prescribed burning treatments. In addition, they also indicated that succession only partially followed the expectation that species with seedbank and rapid dispersal strategies dominate early post-disturbance stages, whereas species with vegetative reproduction strategy prevail in later seral stages (Donelan and Thompson,

1980; Lee, 2004).

#### 4.2. Non-native and native species

It is well-documented that non-native species commonly benefit more from disturbance than natives (Davis et al., 2000; McGlone et al., 2009; Jauni et al., 2015; Pearson et al., 2018; but see McGlone et al., 2011). Hence, it was not surprising to see that non-natives responded more strongly to treatments than did the natives. In this study, we tested one cutting intensity (cut to a basal area of 12 m<sup>2</sup> ha<sup>-1</sup>, as compared to control), and then increased disturbance intensity from there with two burning intensities. Our results indicate that greater intensity disturbances resulted in greater non-native species responses, consistent with previous studies evaluating both cutting and burning (e.g., Griffis et al., 2001; Dodson and Fiedler, 2006; Collins et al., 2007). However, as we show, treatment-induced increases in non-native cover may dissipate over the long-term, with non-natives eventually representing minor community components unless further stimulated by subsequent disturbances (Perchemlides et al., 2008; Kerns et al., 2009).

One way to balance this tradeoff would be to incorporate weed management practices in conjunction with fuels management approaches that anticipate and mitigate such weed invasion. For example, many understory native species in these fire-prone systems recover from fire by vegetatively resprouting (e.g., Lyon, 1971, Lyon and Stickney, 1976), whereas most invaders we encountered (including *C. stoebe*) establish from seed. Hence, use of pre-emergent herbicides in conjunction with fuels treatments could provide a tool for directing post-treatment understory succession in key or strategic areas with high invasion potential, as is being explored in rangeland systems (e.g., Pyke et al., 2014). We caution that such approaches need to be carefully tested for their cascading effects on ecosystem health, but they could provide valuable tools to integrate fuels and weed management for an ecosystem restoration strategy (Kerns et al., 2020). It is possible that after a re-entry treatment, invasive species populations could follow a similar trend to what we observed after the first treatment: an initial spike after treatment, followed by a decline to a low levels of persistence. The unknowns about non-native plant responses related to retreatment highlight the need for continued monitoring when maintenance treatments occur.

Forest overstory cover reduces available understory resources such as light, moisture, and nutrients (Krueger, 1981; Riegel et al., 1992; North et al., 1996; Brais et al., 2004; Jang et al., 2016). Consistent with this, cover (and sometimes richness) of both non-native and native understory groups measured in post-treatment year 23 of our study correlated negatively with basal area of overstory trees at the plot scale (e.g., Belote et al., 2008). Overstory basal area also varied among the treatments as expected, with significantly higher levels in control vs. treated units and a notable trend in the latter towards increased basal area in unburned relative to burned units caused by advanced regeneration therein (Clyatt et al., 2017; Hood et al., 2020). When we controlled for associated variation in tree basal area, differences among treatments were no longer apparent for native understory groups, suggesting that treatment patterns evident in the final year of the study were primarily linked to overstory conditions, i.e., the degree of competitive exclusion by trees. Notably, native understory plants had greatest cover and richness with low overstory densities at the plot scale (as low as 2.0 m<sup>2</sup> ha<sup>-1</sup> in this study), suggesting that forest managers can have substantial influence over native plant recovery simply through cutting, particularly if advanced regeneration as well as invasion of non-native taxa can be managed. In contrast, for non-native taxa, cover remained elevated in burned compared to unburned/control units even when we accounted for the influence of overstory conditions, suggesting that other differences among treatments contributed to final patterns. We suggest that the intensity of the original disturbance (i.e., cutting compounded by burning) was one such factor with persistent impact on non-native plant populations. Overall, these results underscore the

ability of non-native species to exploit multiple disturbances associated with common forest restoration strategies.

#### 4.3. Management implication

Prior work in this system indicates that many of the benefits of restoration treatments on forest structure, composition, and fuel loading have faded 14 to 23 years post-treatment (Clyatt et al., 2017; Crotteau et al., 2018a, 2020; Hood et al., 2020), indicating that retreatments may be warranted at intervals shorter than this study's measurement period and more in line with the range of historic fire occurrence. Short historical mean fire intervals in these dry, low-elevation forests (i.e., approximately 7 years; ranges 3–30 years; Gruell et al., 1982) maintained native understory communities and resilience to fire prior to the introduction non-native species. That said, the most abundant non-native species in our study was *C. stoebe*, a noxious invader known to have strong local-scale impacts on native species (Pearson et al., 2016). Our results indicate that non-native plant responses were still fairly strong 15-years post treatment (Fig. 1), suggesting that retreating this early could exacerbate noxious weed invasions in these forest stands by increasing the frequency of disturbances that seem to benefit non-native more than native taxa. This outcome complicates the manager's role in restoring forests adapted to frequent, low-severity fire by creating a tradeoff between management of fuels (to reduce fire risk) and invasive plant management. Where management objectives are principally focused on promoting resilience to fire, this tradeoff may be a nonissue. However, a manager charged with promoting resilience to fire and restoration of understory communities will need creative and flexible strategies to optimize these objectives.

#### 5. Conclusion

Disturbance from overstory restoration treatments can substantially disrupt understory plant communities and facilitate non-native species invasions. While understories were dynamic over the entire measurement period, we found that peak short-term changes in understory vegetation cover and richness dampened over time and were modest by 23 years after treatment, and that native understory vegetation communities were relatively resilient to restoration treatment in general. Nevertheless, differences between treatments persisted through 23 years of measurement along the gradient of treatment severity, including greater non-native cover in burned treatments than the control. The compounding effect of burning after cutting generally exerted greater impacts on understory vegetation dynamics, especially greater forb cover and diversity. Furthermore, our observed effects of overstory basal area on native understory cover and species richness imply that managing fine-scale overstory density and subsequent regeneration can be used as a tool for regulating understory vegetation. However, the precise nature of burning  $\times$  cutting effects and their differential impact on natives versus non-natives requires further research.

These results provide useful insight into understory vegetation dynamics for forest managers planning restoration of fire-prone forests. Subsequent restoration entries will be necessary to maintain low crown fire hazard and abundant native understory communities, but we caution that there may be tradeoffs between resilience to fire and understory restoration management objectives. While native cover and richness declined between 5 and 15 years post-treatment (which corresponds well with historical fire return intervals), re-treating on such a timeline may amplify non-native species abundance. This research suggests that managers consider a wider array of restoration maintenance options to best achieve specific management objectives, and that additional research and monitoring efforts are required to determine the impacts of re-treatment timing, especially to minimize facilitation of non-native species.

#### CRediT authorship contribution statement

**Woongsoon Jang:** Methodology, Software, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Justin S. Crotteau:** Writing - original draft, Writing - review & editing. **Yvette K. Ortega:** Investigation, Software, Writing - review & editing. **Sharon M. Hood:** Investigation, Data curation, Writing - review & editing. **Christopher R. Keyes:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **Dean E. Pearson:** Investigation, Writing - review & editing. **Duncan C. Lutes:** Investigation, Data curation. **Anna Sala:** 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.

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