

Prescribed fire and conifer removal promote positive understorey vegetation responses in oak woodlands

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Summary

1. Fire-prone woodlands and savannas world-wide face management challenges resulting from fire exclusion and subsequent encroachment of fire-sensitive trees. In the Pacific Northwest (USA), *Quercus garryana* oak woodlands and savannas are threatened by encroachment from the native conifer *Pseudotsuga menziesii* in the absence of fire.

2. In the Bald Hills of Redwood National Park (California, USA), prescribed fire and conifer removal have been used to restore encroached woodlands. We examined the effects of encroachment and restoration on understorey vegetation, comparing four treatments: prescribed fire, prescribed fire and conifer removal, conifer removal, and encroached (control).

3. Treatments including prescribed fire had the greatest native species richness. These two treatments also had the greatest non-native species richness, at both the site level and the treatment level. Woodlands treated with conifer removal and no prescribed fire were intermediate in species richness and diversity compared to burned treatments and encroached woodlands. Encroached woodlands had diminished richness and diversity compared to all restoration treatments. Non-metric multidimensional scaling (NMS) ordination demonstrated that conifer basal area, conifer litter and fine wood were associated with low species richness and diversity and that elevation and thatch were associated with higher species richness and diversity. Indicator species analysis identified that most native species and non-native species were associated with burned woodlands that were never encroached.

4. *Synthesis and applications.* Our results suggest that both prescribed fire and conifer removal have benefits for understorey plant communities, increasing species richness, diversity and cover in oak woodlands and shifting understorey communities from forest-associated species to more woodland-associated species. Restoration of remnant *Quercus garryana* oak woodlands is complicated by the persistence and abundance of non-native herbaceous plants.

Key-words: conifer encroachment, ecological restoration, non-metric multidimensional scaling, non-native species, oak woodlands, Oregon white oak, prescribed fire, *Pseudotsuga menziesii*, *Quercus garryana*, understorey vegetation

Introduction

Fire has played a major role in creating and maintaining woodlands, savannas and grasslands world-wide (Scholes & Archer 1997; Mayer & Khalyani 2011; Staver, Archibald & Levin 2011). Many of these ecosystems are

considered alternative stable states maintained by interactions between vegetation, climate and fire (Beckage, Platt & Gross 2009). Where fires are frequent, trees with fire-adapted traits are capable of persisting; where fires are infrequent or excluded, fire-sensitive woody plants invade and alter ecosystem structure and processes (Scholes & Archer 1997; Briggs *et al.* 2005). Grasslands, savannas and woodlands world-wide provide numerous examples of the tree encroachment phenomenon (e.g. Cowling, Pierce & Moll 1986; Briggs *et al.* 2005; Price & Morgan 2008).

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These ecosystems share a commonality; when fire is excluded, trees and shrubs become more dominant.

The process of encroachment may result in a range of ecological consequences including reduction in landscape heterogeneity (Devine, Harrington & Peter 2007; Brudvig & Asbjornsen 2009), changes to soil chemistry (Hibbard *et al.* 2001; Griffiths, Madritch & Swanson 2005) or animal community structure (Alford *et al.* 2012), alteration of carbon storage capacity (Jackson *et al.* 2002) and changes to understorey community structure (del Moral & Deardorff 1976; Foster & Schaff 2003). Reduced species richness resulting from encroachment has been documented in many plant communities, including woodlands in Australia (Price & Morgan 2008), grasslands in western Washington (Foster & Schaff 2003), tallgrass prairie in north-east Kansas (Lett & Knapp 2005) and blackland prairies in Mississippi (Weiher *et al.* 2004). Restoration of encroached ecosystems usually involves removal of encroaching shrubs and trees by mechanical methods or girdling, the reintroduction of fire or a combination of these methods (Devine, Harrington & Peter 2007; Perchemlides, Muir & Hosten 2008; Brudvig & Asbjornsen 2009). Although removing encroaching species to maintain a vegetation type is often a priority for land managers, the efficacy of restoration treatments for restoring understorey communities is rarely tested.

We studied understorey vegetation response to restoration treatments in *Quercus garryana* Hook. Oregon white or Garry oak woodlands and savannas of the Pacific Northwest (USA and Canada). These communities have long histories of both lightning- and Native American-ignited fires (Agee 1996; Hosten *et al.* 2006). When maintained by fire, *Q. garryana* savannas and woodlands have a sparse overstorey and a diverse understorey dominated by fire-tolerant grasses and forbs (Tveten & Fonda 1999; Devine, Harrington & Peter 2007). A consequence of fire exclusion is that young *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* Douglas-fir saplings, formerly killed by frequent fires, establish and grow among sparse-canopied, shade-intolerant oaks (Agee 1996; Engber & Varner 2012). In fire-free intervals, *P. menziesii* pierce through oak crowns, leading to crown dieback and eventual mortality of the shorter-statured oaks (Barnhart, McBride & Warner 1996; Devine & Harrington 2006). This results in open oak savannas and woodlands transitioning to closed-canopy *P. menziesii* forests (Engber *et al.* 2011). The encroachment process facilitates a feedback cycle that supports further vegetation change as the understorey composition shifts to favour shade-tolerant forbs and the understorey microclimate is altered (Devine, Harrington & Peter 2007; Engber *et al.* 2011). Flammable herbaceous vegetation and oak leaf litter are replaced by compact conifer litter and coarse woody fuels (Engber *et al.* 2011). The shade generated by the conifer canopy increases moisture retention, making invaded woodlands less suited to the spread of subsequent fires (Engber *et al.* 2011), a process analogous to positive feedbacks observed in

eastern North America *Quercus* woodlands (Nowacki & Abrams 2008) and negative feedbacks observed in other savannas and woodlands around the world (Beckage, Platt & Gross 2009; Staver, Archibald & Levin 2011).

Our study focused on oak woodlands in the Bald Hills of Redwood National Park in north-western California. The Bald Hills encompass oak woodlands and prairies interspersed with mixed-evergreen, *P. menziesii* and *Notholithocarpus densiflorus* (Hook. & Arn.) tanoak forests in fire-protected sites. An estimated 29–44% of woodlands and prairies in the Bald Hills have been lost to conifer encroachment since 1850 (Sugihara & Reed 1987b; Fritschle 2008). To restore and maintain oak woodlands, park managers began restoration treatments in 1981 (Sugihara & Reed 1987a). Restoration treatments included prescribed fire (at 3- to 5-year intervals), mechanical removal or girdling of all large (>c. 45 cm dbh) *P. menziesii* or a combination of both. Other encroached woodlands were left untreated. The result of these concurrent management techniques is a mosaic of treatments, and combinations of treatments, which span c. 30 years.

Few studies have examined the response of understorey vegetation to encroachment and restoration treatments, and only one study has considered the effects of conifer removal in *Q. garryana* woodlands (Devine, Harrington & Peter 2007). The objective of this study was to assess the response of understorey vegetation to conifer encroachment and treatments used to restore *Q. garryana* woodlands. Using treatments that spanned a restoration gradient from frequently burned open oak woodlands to fire-excluded, heavily encroached forests, we asked the following questions: (i) Do species richness, diversity and composition differ among the treatments? (ii) Does the cover of native and non-native species differ among the treatments? and lastly (iii) Where changes are detected, what are the potential environmental factors driving these changes (e.g. canopy cover, litter, basal area)? The results of this study will help managers in *Quercus garryana* woodlands and other ecosystems encroached by shade-tolerant conifers evaluate the effectiveness of restoration treatments on understorey vegetation.

Materials and methods

STUDY AREA

Study sites were within the Bald Hills of Redwood National Park (41°2', –123°9'). The Bald Hills contain 1700 ha of grasslands and oak woodlands located on upper south- and west-facing slopes (Redwood National Park 1992). *Pseudotsuga menziesii* and *N. densiflorus* forests historically occupied fire-sheltered woodland and grassland margins, lower slopes, riparian areas and north-facing slopes, and thus, encroachment tends to initiate at lower elevations and move upward. The climate of the region is Mediterranean. The 30-year average (1983–2012) annual rainfall is 2700 mm, with 96% of the precipitation falling between October and May (PRISM Climate Group; [© 2016 The Authors. Journal of Applied Ecology © 2016 British Ecological Society, *Journal of Applied Ecology*](http://</p>
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www.prism.oregonstate.edu, accessed January 2016). The year of our study was especially wet with 3900 mm of rain. In early spring of 2012, more than double the 30-year average rainfall occurred in March, and substantially more rain than average occurred in April. The 30-year average monthly temperatures range from 7.3 to 19.3 °C. The minimum and maximum average monthly temperatures were slightly more extreme in 2012 (5.5–20.2 °C). A strong Pacific Ocean influence produces summer fog that usually clears by late morning (Redwood National Park 1992). Soils in the Bald Hills consist primarily of xeralfs and umbrepts, the latter most susceptible to *P. menziesii* invasion (Redwood National Park 1992).

Prior to European American settlement, the Chilula and the Yurok Tribes engaged in widespread burning of the Bald Hills (Underwood, Arguello & Siefkin 2003; Hosten *et al.* 2006). European settlers began grazing sheep and cattle in the late 1860s (Underwood, Arguello & Siefkin 2003). Although domestic livestock grazing ended with the Park's acquisition of the Bald Hills in 1978, many non-native grass and forb species introduced during this era persist and have become widespread (Redwood National Park 1992). Native Roosevelt elk *Cervus elaphus roosevelti* and black-tailed deer *Odocoileus hemionus* inhabit the Bald Hills and selectively graze the prairies and woodlands.

RESTORATION TREATMENTS AND STUDY DESIGN

We selected 24 study sites, with six sites in each of four treatment categories: encroached woodlands; encroached woodlands treated with conifer removal (removal only); encroached woodlands treated with both conifer removal and prescribed fire (burned with removal); and woodlands that were never encroached that have been consistently burned (burned only). Prescribed burning in the Bald Hills typically occurs between September and November. Fire weather prescriptions dictate burn days and typically ensure lower-intensity burns resulting in mortality of *P. menziesii* < 3 m in height, and generally not affecting larger *P. menziesii* or more fire-tolerant *Q. garryana* (Engber *et al.* 2011). The number and intensity of prescribed fires varied for sites in the burned treatments; two sites in each treatment had been burned twice, and four sites in each treatment had five or six burns. There were no major differences between the sites in terms of proximity to potential propagules or refugia for native or non-native species. The study area spanned 6.5 km from the most north-western site to the most south-eastern and elevations from 495 to 927 m above mean sea level.

Our study design was opportunistic, with past restoration work dictating site locations. While this design had the advantage of utilizing actual restoration treatments, this design restricted us from having treatments encompassing sites with matching periods of time since treatment. In woodland categories involving conifer removal, time since treatment varied from 11 to 21 years for eleven of the twelve sites, and in some sites, conifers were removed in successive treatments over a span of several years. In one site with conifer removal only, removal occurred 4 years prior to the study. We assessed the opportunistic nature of the study design and potential for spatial autocorrelation and its influence on vegetation patterns with a hierarchical, agglomerative cluster analysis (McCune & Mefford 2011) performed on frequency of all species at all sites using Sørensen distance and nearest neighbour group linkage. The resulting dendrogram suggested that vegetation patterns were driven by treatment rather than spatial proximity of

sites (see Appendix S1 in Supporting information). This analysis underscored our confidence in site selection despite the opportunistic nature of the study design.

FIELD DATA COLLECTION

We sampled vegetation between 02 June and 03 August 2012 coinciding with the primary flowering and fruiting period (Saenz & Sawyer 1986). At each of the 24 sites, 15 1 × 1 m quadrats were haphazardly tossed within the treatment boundaries, starting from locations that were central to, and representative of the treatment types. We assessed species area curves to determine that our sampling intensity was adequate. In encroached sites treated with patchy conifer removal, we sampled vegetation within a c. 10 m radius of stumps or girdled *P. menziesii* to isolate the understorey response to the treatment. In treatments without conifer removal, these constraints were unnecessary. We avoided edges, riparian areas, wet depressions, rock outcrops and roadsides. We recorded slope (%), aspect, UTM coordinates and elevation at each plot. Aspects were converted to folded aspect (radians E of N) and direct incident radiation (MJ cm⁻² year⁻¹) and calculated the heat load index (McCune & Keon 2002) for each site to assess effects on vegetation.

We identified plant species following the nomenclature of Baldwin *et al.* (2012). Absolute aerial cover of each species was estimated using the Bailey & Poulton (1968) cover scale, with cover values of 0–1%, 2–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100%. Cover data for species and plots were averaged to the site level using the midpoint of each cover class. Shannon's diversity index (H') was calculated for each site (Magurran 2004). H' considers the number of species and their evenness, with higher values indicating sites with more species that are evenly distributed (Magurran 2004).

To evaluate the effects of the treatments on understorey vegetation, absolute cover of ground cover categories including thatch (defined as dead plant material between growing plants and soil); oak leaf litter, conifer litter, fine wood (< 2.54 cm diameter); large wood (≥ 2.54 cm diameter); and bare ground was measured for each plot using the Bailey & Poulton (1968) cover scale (Elzinga, Salzer & Willoughby 1998). We averaged ground cover data for each plot to the site level using the midpoint of the cover classes. We estimated canopy closure at each plot via the average of four measurements (%) using a concave spherical densiometer (Lemmon 1956). We estimated overstorey basal area of all trees using a prism (basal area factor = 2.23 m² ha⁻¹) over plot centre. For each species, we tallied live and dead trees, as well as dead girdled trees and live girdled trees.

DATA ANALYSIS

Understorey vegetation response to treatment categories was evaluated by comparing the mean absolute cover, diversity and richness of the sites among treatments with ANOVA using the R package pgirmess (Giraudoux 2013). Similarly, we compared environmental variables potentially affecting understorey vegetation for the six sites in each treatment category using ANOVA. When significant treatment effects were found ($\alpha = 0.05$), we conducted pairwise comparisons between individual treatments using Tukey's HSD test. Residual plots were examined to assess normality and homogeneity of variance. If data failed to meet assumptions of normality and homoscedasticity, they were

transformed using first a square root transformation, then a logarithmic transformation (with 1.0 added to eliminate zero values; Zar 1999). If assumptions for ANOVA were still violated, we used a nonparametric Kruskal–Wallis test on ranks. We assessed relationships between potential environmental drivers of understorey vegetation using nonparametric Spearman rank correlations (r_s). Vegetation response variables included absolute cover by native and non-native life form groups of graminoids, forbs and shrubs, total richness and H' .

We assessed differences in composition of woodland understorey plant communities between restoration treatments using non-metric multidimensional scaling (NMS) ordination in PC-ORD version 6.0 (McCune & Mefford 2011). NMS is a nonparametric, iterative technique that uses ranked distances to arrange values (in this case study sites and species), along a number of axes determined by reducing 'stress' (McCune & Grace 2002). Axis values were generated with Euclidean distance, using a random starting configuration and 100 maximum iterations. We restricted the species to those that occurred in at least one quadrat in at least three of the 24 sites, or 12.5% frequency. We compared our axis scores with environmental data using Pearson correlations to explore which factors most influenced vegetation, and we show relatively strong relationships ($r \geq 0.5$) using joint plots.

To evaluate differences in community composition among treatments, we used nonparametric permutation MANOVA (PERMANOVA) in PC-ORD version 6.0 (McCune & Mefford 2011). PERMANOVA is a multivariate analysis of variance which uses permutation procedures of reshuffling treatment labels to generate a null distribution. The outputs are probabilities based on comparing the null distribution to the original F statistic obtained from the real ordering of the data relative to the treatment (McCune & Grace 2002). Sørensen's distance was used for this test, with 4999 permutations (McCune & Mefford 2011). To detect species with high fidelity to a particular treatment, we performed indicator species analysis in PC-ORD version 6.0 (McCune & Mefford 2011). Frequency values were used to calculate

indicator values for each species. Indicator values range from 0 to 100, with 100 representing a species exclusively associated with a treatment. A Monte Carlo test with 5000 randomizations (McCune & Mefford 2011) was used to obtain the probability of generating an indicator value equal to or greater than one obtained by chance.

Results

We found 161 vascular plant species across the four woodland treatments, including eight trees, 13 shrubs, 102 forbs, 35 graminoids and three ferns. All tree and fern species were native, and all shrubs species were native except one. Twenty-three of the 102 forbs and 22 of the 35 graminoids were non-native. Fifteen additional species were observed during the study but never occurred in plots (13 native and two non-native). Woodlands burned with removal had a mean of 14.9 species per 1 m² quadrat, followed by burned only with 14.4, removal only with 13.0 and encroached woodlands with only 5.1 species (Table 1).

Woodlands with removal only generally had vegetation metrics that were intermediate between encroached woodlands and the two burned categories (Table 1). No differences in richness were found between burned only and burned with removal treatments. Encroached woodlands had lower understorey plant species richness than the other treatments with a mean of only 26.3 species per site ($F = 10.3$, d.f. = 3, $P < 0.001$). Woodlands with removal had 66.5% greater richness than encroached woodlands, followed by burned only which had 81.4% greater richness, and burned with removal which had double (*c.* 99.6%) the species richness of encroached woodlands. Encroached woodlands also had lower understorey plant

Table 1. Species richness and Shannon diversity index (mean \pm 1.0 SE) among woodland treatments in the Bald Hills of Redwood National Park

Variable	ENC	REM	REMRX	RX	ANOVA <i>P</i> -value	K–W <i>P</i> -value
Plot-level mean richness						
All species (mean at 1 m ²)	5.1 (0.5)	13.0 (0.4)	14.9 (0.4)	14.4 (0.3)		
Site-level mean richness						
All species	26.3 (3.4) ^a	43.8 (2.3) ^b	52.5 (4.2) ^b	47.7 (4.0) ^b	< 0.001	
Native	23.3 (3.3)	30 (2.5)	34.8 (4.0)	29.5 (3.7)	0.155	
Non-native	1.7 (0.4) ^a	12.7 (0.8) ^{ab}	16.6 (1.7) ^b	17.3 (0.8) ^b		< 0.001
Native forb	13.7 (2.1)	17.5 (2.2)	21.3 (2.9)	19.2 (2.7)	0.190	
Non-native forb	0.8 (0.2) ^a	6.5 (0.7) ^b	8.5 (0.8) ^b	7.5 (0.7) ^b	< 0.001	
Native grass	2.3 (0.7) ^a	4.7 (0.3) ^b	4.0 (0.6) ^{ab}	5.8 (0.5) ^b	< 0.01	
Non-native grass	0.8 (0.3) ^a	6.2 (0.6) ^b	7.8 (1.0) ^{bc}	9.8 (0.4) ^{bc}	< 0.001	
Site-level diversity						
Shannon diversity index (H')	3.0 (0.2) ^a	3.4 (0.1) ^b	3.6 (0.1) ^b	3.5 (0.1) ^b	< 0.01	
Treatment level richness						
All species	66	98	121	119		
Native species	55	61	80	78		
Non-native species	11	37	41	41		

ENC = encroached; REM = removal only; REMRX = burned with removal; RX = burned only.

The *P*-values represent the results of ANOVA or nonparametric Kruskal–Wallis test on ranks. Different superscript letters indicate significant differences between treatments based on results from Tukey–Kramer multiple comparison tests and nonparametric Kruskal–Wallis (K–W) multiple comparison tests.

diversity values (Shannon index; $P < 0.01$; Table 1) than the other treatments; all pairwise comparisons were significant ($P < 0.05$). Woodlands burned with removal had the highest diversity, followed by burned only, removal only and encroached woodlands.

Native and non-native plant species richness varied by treatment. Encroached woodlands had fewer non-native species ($P < 0.001$) than the two burned treatments (Table 1). Encroached sites had a mean 1.6 non-native species m^{-2} , followed by removal only (12.6), burned with removal (16.5) and burned only (17.3). Much of the increase in non-native species richness from encroached woodlands to the burned categories was attributable to an increasing number of non-native grass species. Encroached woodlands also had the fewest native species (23.3), followed by burned only (29.5), removal only (30.0) and burned with removal (34.8) (Table 1). Although the number of native species was not significantly different when averaged at the site level, when unique species from all the sites are combined by treatment, the woodland categories that include prescribed fire had more unique native species. These two categories also had the greatest richness either when averaged at the site level or when combined at the treatment level (Table 1).

Several measures of understorey plant cover increased from encroached woodlands to those with removal only, to the two burned treatments (Table 2). Encroached sites had less understorey cover (mean = 25%) than the other treatments ($P < 0.01$), all of which had at least twice this cover (Table 2). Non-native cover also followed this trend, with encroached sites having the lowest non-native cover (0.2%), which differed ($P < 0.01$) from burned with removal (23.3%) and burned only (26.5%).

Native cover did not differ among the treatments (Table 2). Cover of native forbs increased along the gradient from encroached woodlands, to removal only, to the categories with fire, though no significant differences were

found ($P = 0.140$; Table 2). Non-native forb cover was lower in encroached woodlands than in the burned woodland categories ($P < 0.01$). Encroached sites had lower native grass cover ($P < 0.01$) and non-native grass cover ($P < 0.001$; Table 2) than the two burned categories. Though not significant ($P = 0.07$), the cover of native perennial forbs in the burned with removal category was nearly double the cover in encroached woodlands and woodlands with removal only (Table 2).

Among environmental variables of elevation, slope, aspect, heat load and direct incident radiation, only elevation differed among treatments ($P < 0.001$) (see Table S1). The mean elevation of burned only woodlands was higher than encroached and removal only; removal only sites were lower than burned with removal.

Woodland overstorey composition and structure differed across the treatments. Overstorey canopy cover in encroached woodlands averaged 96%, and differed from the other treatments which ranged from 70 to 79% ($P < 0.01$; see Table S1). Encroached woodlands had greater total basal area than the other treatments ($P < 0.001$), dominated (56% of mean basal area) by *P. menziesii*. *Pseudotsuga menziesii* snag basal area was greatest in sites with removal only ($P < 0.05$). Burned only had the greatest oak basal area and differed from encroached woodlands and burned with removal treatments ($P < 0.01$).

Several overstorey and ground cover attributes associated with specific treatments were highly correlated with vegetation measures (see Table S2). Basal area of living *P. menziesii* was strongly and negatively correlated with species richness, Shannon's diversity, cover of non-native grasses and forbs, total non-native cover, native grass cover and total cover (all $P < 0.001$). Overstorey canopy cover was strongly and negatively correlated with species richness, Shannon's diversity, cover of non-native grasses and forbs (native and non-native) and total cover (both

Table 2. Absolute understorey plant cover (means \pm 1.0 SE) for woodland treatments in the Bald Hills of Redwood National Park

Cover variable	ENC	REM	REMRX	RX	ANOVA P -value	K-W P -value
Total	25.2 (9.6) ^b	51.5 (5.2) ^{ab}	68.5 (5.1) ^a	59.9 (6.6) ^a	< 0.01	
Native	24.9 (9.6)	36.2 (7.1)	45 (6.4)	33.1 (6.9)	0.340	
Non-native	0.2 (0.1) ^b	14.3 (3.3) ^{ab}	23.3 (4.4) ^a	26.5 (2.1) ^a		< 0.01
Native forb	11 (0.3)	14.1 (2.6)	19.9 (0.3)	15.3 (0.2)		0.140
Non-native forb	0.1 (0.04) ^b	4.7 (1.2) ^{ab}	7.2 (1.6) ^a	5.3 (0.7) ^a		< 0.01
Native grass	0.6 (0.2) ^b	1.5 (0.3) ^{ab}	6.1 (4.0) ^a	5.6 (2.3) ^a	< 0.01	
Non-native grass	0.07 (0.1) ^b	9.6 (2.2) ^{ab}	16.2 (2.9) ^a	21.2 (1.8) ^a		< 0.001
Native annual grasses	0 (0.0)	0 (0.0)	0 (0.0)	0.006 (0.0)		0.390
Non-native annual grasses	0.01 (0.0) ^b	5.8 (1.2) ^a	9.3 (2.1) ^a	9 (1.7) ^a	< 0.001	
Native perennial grasses	0.6 (0.2) ^b	1.5 (0.3) ^{ab}	6.1 (4.0) ^a	5.6 (2.3) ^a	< 0.01	
Non-native perennial grasses	0.06 (0.0) ^b	3.8 (1.1) ^{ab}	6.9 (3.6) ^{ab}	12.0 (2.6) ^a		< 0.001
Native perennial forbs	9.6 (5.2)	9.4 (1.8)	17.9 (3.1)	13.8 (2.2)		0.070
Non-native perennial forbs	0.0 (0.0) ^b	3.1 (0.9) ^a	3.6 (0.9) ^a	2.8 (1.0) ^{ab}		< 0.01

ENC = encroached; REM = removal only; REMRX = burned with removal; RX = burned only.

The P -values represent the results of ANOVA or nonparametric Kruskal–Wallis test on ranks. Different superscript letters depict significant differences between treatments based on results from Tukey–Kramer multiple comparison tests and nonparametric Kruskal–Wallis multiple comparison tests.

native and non-native; all $P < 0.05$). In addition to being negatively correlated with conifer basal area and canopy cover, understorey species richness was also strongly and negatively correlated with conifer litter, basal area of all trees and fine wood (all $r_s > -0.51$, $P < 0.05$), and strongly and positively correlated with thatch cover ($r_s = 0.67$, $P < 0.001$). Shannon's diversity was strongly and negatively correlated with total and conifer tree density, canopy cover, conifer litter and fine wood (all $r_s > -0.50$, $P < 0.001$).

The NMS ordination was best fit by a two-axis solution (final stress = 9.14; final instability = 0.00019), and the four treatment groups formed distinct clusters (Fig. 1). In agreement, PERMANOVA demonstrated that community composition differed across treatments ($F = 7.5$, d.f. = 3, $P < 0.001$). Pairwise comparisons showed that encroached sites differed significantly from all other treatments, and sites with removal only were also significantly different from burned only (all $P < 0.01$). In addition, burned only and burned with removal differed from each other ($P = 0.01$).

The first axis in the ordination accounted for 89.5% of the variation and was strongly associated with live *P. menziesii* basal area, total tree basal area, conifer litter cover and fine wood cover (Fig. 1; see Table S3). These factors, along with canopy cover, were strongly and positively correlated with the six encroached sites. On the opposite end of this gradient, thatch cover and elevation were correlated with burned with removal and burned only woodlands. The second NMS axis, accounting for an additional 4.7% of the variation, was weakly correlated with canopy cover. Sites with higher canopy cover were

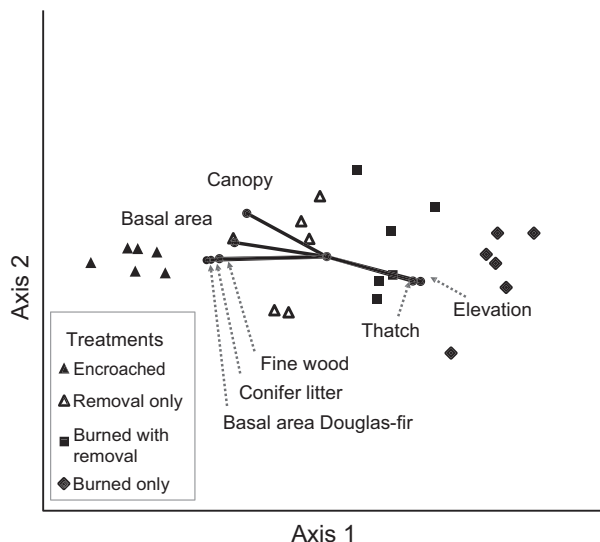


Fig. 1. Understorey vegetation response by treatment based on a non-metric multidimensional scaling ordination. Environmental data were overlaid as joint plots to show variables most responsible ($r \geq 0.5$) for separation of sites and treatment categories in species space. Most of the variation was explained with a two-axis solution: Axis 1 (89.5%) and Axis 2 (4.7%).

associated with higher axis 2 values, while sites with lower canopy cover had lower values.

Indicator species analysis identified several species associated with particular treatments (see Table S4). Three native understorey forbs had significant indicator values for encroached sites. Two native species, a forb and a shrub, had high indicator values for removal only sites. *Cirsium vulgare* (Savi) Ten., a non-native thistle, had a high indicator value for woodlands burned with removal, as did one native forb (see Table S4). Burned only sites had twelve species with significant indicator values. Six non-native species had a high fidelity to this treatment including three perennial, invasive, non-native grasses, one invasive annual grass and two non-native annual forbs. Six native species had high fidelity to this treatment including the native sedge *Carex tumulicola* Mack., *Elymus glaucus* Buckley, a native perennial grass, *Luzula comosa* E. Mey., a native woodrush, and three native forbs.

Discussion

Our study provides evidence that both conifer removal and prescribed burning can effectively restore understorey plant communities in an oak woodland setting. In *Q. garryana* woodlands in the Bald Hills, where encroachment by *P. menziesii* has greatly altered understorey communities, burning and conifer removal treatments increased species richness and cover (Table 1). In addition, these treatments substantially altered the suite of understorey species as compared to encroached treatments. Though both burning and conifer removal were effective, treatments that included burning were more effective than conifer removal alone. Woodlands treated with conifer removal and no prescribed fire were intermediate in species richness and diversity compared to woodlands that were either burned or burned with conifer removal. These results add to a body of literature concerning fire-excluded woodlands and prairies (Brudvig & Asbjornsen 2009; Alford *et al.* 2012; Lettow *et al.* 2014), which has found that restoration treatments following encroachment can successfully shift understorey communities towards higher herbaceous species richness and diversity, and from more forest-associated species to more woodland or savanna-associated species.

EFFECTS OF CONIFER ENCROACHMENT ON UNDERSTOREY PLANTS

Fewer understorey species were associated with sites encroached by *P. menziesii*. These species are characterized by shade tolerance and typically occur in mesic forests of the region (Pojar, MacKinnon & Alaback 1994; Coupé *et al.* 1996; Baldwin *et al.* 2012). *Pseudotsuga menziesii* encroachment in western Washington oak woodlands has been linked to replacement of a diverse suite of prairie species with a smaller set of mesophytic species

(del Moral & Deardorff 1976), and a rapid shift from grassland to forest species, with a dramatic (75%) decrease in richness 27 years later (Foster & Schaff 2003). Encroached woodlands had the greatest relative number of native species and the lowest relative number and cover of non-native species. Fewer non-native species and lower richness have been found in other *P. menziesii* understoreies compared to neighbouring *Q. garryana* woodlands (Thysell & Carey 2001). The deep shade and cooler temperatures beneath *P. menziesii* likely restrict species with a narrow range of shade tolerance including many non-natives (Thysell & Carey 2001). Although non-native species are less prevalent with encroachment, this process profoundly diminishes native woodland and prairie flora (del Moral & Deardorff 1976; Foster & Schaff 2003).

In contrast, the high understorey plant diversity in oak woodlands is likely dependent on gradients of light and soil moisture characterized by alternating canopy cover and openings in woodland overstoreies (Hutchinson *et al.* 2005; Brudvig & Asbjornsen 2009). Fire exclusion and subsequent encroachment cause these gradients to become more homogeneous, altering habitat formerly suitable to a wider range of species (Brudvig & Asbjornsen 2009). Conifer encroachment also increases forest floor litter and humus, favouring a different suite of species less adapted to fire (del Moral & Deardorff 1976; Devine, Harrington & Peter 2007; Engber *et al.* 2011). This addition of conifer litter most likely causes significant changes to soil properties, including rates of nutrient cycling, microbial activity and moisture-holding capacity (Hibbard *et al.* 2001; Griffiths, Madritch & Swanson 2005), and these have the potential to influence the community of understorey plants.

THE ROLE OF FIRE IN RESTORING OAK WOODLANDS

The two burned woodland treatments had the greatest understorey species richness. Native species richness was similar for the three restored woodland categories when averaged at the site level, but when combined at the treatment level, native richness was greatest for the two burned treatments. The two burned treatments also had more non-native species at the site level and at the treatment level, demonstrating that burning favours many native species, as well as many widespread non-natives. Additionally, indicator species analysis revealed twelve species with high fidelity to burned only woodlands; four of these species (three native and one non-native) possess traits of fire-adapted plants (Livingston 2014).

Fire may influence understorey richness and composition in several ways, including reducing competition and shading from neighbouring plants (Maret & Wilson 2005) and altering soil nutrients, particularly available nitrogen (Agee 1996). In fire-dependent ecosystems, fire removes litter and thatch (Peterson & Reich 2008) that can impede germination and reduce survival of light-demanding herbs (Maret & Wilson 2005; Devine, Harrington & Peter 2007; MacDougall & Turkington 2007). Woodlands in the

burned with removal category likely benefited from the consumption of conifer litter and conifer debris compared to woodlands with removal only. Both burned woodland categories also benefit from the periodic consumption of oak litter and thatch, contributing to higher richness and diversity. Similar increases in species richness have been reported with the return of fire to other North American savannas and woodlands (e.g. White 1983; Griffis *et al.* 2001; Hutchinson *et al.* 2005).

Plant community differences between burned only woodlands and woodlands burned with removal are complex. In the Bald Hills, these categories were similar when individual vegetation metrics were analysed, yet composition differences were detected with the PERMANOVA. Additionally, indicator species analysis revealed that burned only woodlands had more species with high fidelity. In addition to encroachment and treatment effects, differences in community composition may be influenced by ecological factors including frequency and intensity of fires (Agee 1996; Peterson & Reich 2008), microsite conditions (Grenier 1989), local seed dispersal and the legacies of historic livestock grazing (Saenz & Sawyer 1986; Grenier 1989). Our opportunistic study design was unable to discern these factors. Future work could focus on the differences between these treatments widely prescribed in woodland restoration.

INVASIVE SPECIES IN WOODLAND RESTORATION

Many woodlands and savannas in the Pacific Northwest are dominated by non-native annual and perennial species as a result of intentional introductions, grazing of non-native livestock, fire exclusion and other disturbances (Agee 1996; Hosten *et al.* 2006). Livestock grazing in the Bald Hills resulted in the introduction of many non-native grass and forb species (Saenz & Sawyer 1986; Sugihara, Reed & Lenihan 1987). Cattle removal allowed non-native perennial species to out-compete most native grasses diminished during intensive grazing. The exclusion of livestock grazing shifted much of the non-native, annual-dominated flora to a non-native, perennial-dominated flora, with localized native species dominance beneath oak canopies (Saenz & Sawyer 1986; Engber *et al.* 2011). Current disturbances such as road building, logging and ranching on adjacent properties continue to provide pathways for non-native species.

Restoration treatments without the addition of prescribed fire have resulted in increased cover of non-native species in other oak woodlands (Devine, Harrington & Peter 2007; Perchemlides, Muir & Hosten 2008). Where oak woodland understoreies are dominated by non-native species, prescribed burning may only serve to maintain the undesirable species composition (Tveten & Fonda 1999). There is considerable uncertainty regarding the ecosystem consequences of this non-native persistence in oak woodlands, but there may be far-reaching effects on ecosystem composition and processes (Agee 1996; Livingston & Varner 2016).

RESTORATION AND MANAGEMENT IMPLICATIONS

Ecological restoration treatments in *Q. garryana* woodlands were associated with dramatic increases in understory diversity and richness and shifts from forest-associated to woodland or savanna-associated species. These results should encourage land managers of other encroached ecosystems who are concerned with restoring understory communities. Conifer removal alone resulted in the return of some woodland species and rebounds in diversity and richness, while the addition of prescribed burning resulted in greater rebounds. To overcome the persistence of non-natives, sowing native seeds, particularly combined with prescribed burning (Maret & Wilson 2005; Stanley, Dunwiddie & Kaye 2011) or planting native perennials (Vance, Neill & Morton 2006), may be warranted. Although complicated by the presence of non-native species, treatments of conifer removal and prescribed fire are effective at maintaining *Q. garryana* woodlands and their diverse native plant understories. Given the extent of woodlands and savannas that are being lost to encroachment world-wide (Scholes & Archer 1997; Sahara *et al.* 2015), evaluation of restoration techniques is likely to be a growing priority for ecologists.

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Data accessibility

Sampling data and spatial data are available at the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.4s209> (Livingston *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Topographic variables and ground cover for woodland categories.

Table S2. Spearman correlations between environmental variables and plant cover estimates, richness and diversity for oak woodlands.

Table S3. Pearson's correlation coefficients showing the relationship of environmental variables to ordination axes for study sites.

Table S4. Indicator species analysis on frequency values for individual species associated with particular treatments.

Appendix S1. Dendrogram of sites based on frequency of all species.