



## Tamm Review

## Effects of tree cutting and fire on understory vegetation in mixed conifer forests

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## ABSTRACT

Mixed conifer forests of western North America are challenging for fire management, as historical fire regimes were highly variable in severity, timing, and spatial extent. Complex fire histories combined with site factors and other disturbances, such as insect outbreaks, led to great variation in understory plant communities, and management activities influence future dynamics of both overstory and understory communities. This variation needs to be considered as part of ecosystem-scale efforts to influence future fires and restore the composition and structure of mixed conifer forests. We undertook a systematic review of published studies evaluating effects of tree cutting and fire on understory vegetation in western North American mixed conifer forests. Forty-one studies, published in 50 articles, met inclusion criteria and encompassed projects in seven states in the USA and British Columbia in Canada. Total understory plant abundance (cover, biomass, or density) commonly declined in the short term within 4 years after treatment. This may result from damage to plants during tree cutting operations or fire, heavy loadings of slash, little change or even expansion of tree canopies after low-intensity treatments, herbivory, or drought. In contrast, all 7 studies measuring understories longer than 5 years since treatment reported increases in understory metrics. Treatments in these long-term studies also persistently decreased tree canopy cover. Most or all native species endured (even if reduced in abundance) through cutting operations or fire. A model of understory response has emerged that treatments generally do not eliminate species, and often benefit species absent or uncommon in untreated forest. Groups of native species (e.g., *Epilobium* spp.) appear fire-dependent, because they are uncommon or absent in unburned mixed conifer forests and after tree cutting alone. Cutting and prescribed fire applied together resulted in the greatest invasion of non-native plants, but non-native cover was minimal compared to native cover. Few studies examined influences of intensity of tree cutting or severity of prescribed fire, but overstory-understory relationships suggest that treatments must substantially reduce overstory density from maximum values (which can exceed 3000 stems ha<sup>-1</sup> and 80 m<sup>2</sup> ha<sup>-1</sup> basal area) and tree canopy cover to <30–50% cover to elicit appreciable responses from the forest understory. Few studies examined understory dynamics after wildfire relative to unburned forest, and further work is warranted because wildfire is a likely eventual outcome of passive management in these forests. Across a broad region from the southwestern United States into Canada, prescribed fire and tree cutting consistently increased disturbance-promoted native species in the short term and total understory abundance in the long term. Active management using tree cutting and fire will likely benefit both biodiversity conservation and fire management in current mixed conifer forests.

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## 1. Introduction

Conserving forest biodiversity and maintaining ecosystem services is challenging forest managers globally (Honnay et al., 2002; Hart and Chen, 2006; Paillet et al., 2010). Meeting this challenge benefits from a comprehensive understanding of the effects of a range of forest management activities – including passive management – on ecosystem components (Metlen et al., 2004; North et al., 2007; Kalies et al., 2010). Understory plant communities are a critical forest component containing a major proportion of forest species diversity and providing numerous ecosystem functions that can both affect and be affected by forest management activities (Roberts, 2004; Gilliam, 2007; Barbier et al., 2008). Tree cutting and fire are two of the main management activities affecting forest understory dynamics (Selmants and Knight, 2003; Ares et al., 2010; Halpern and Lutz, 2013). For example, different methods of tree cutting can differentially influence understories, and a particular cutting method could affect plant cover differently than it affects species richness (Dodson et al., 2007; Kreyling et al., 2008; Knapp et al., 2013). Similarly, plant groups, such as native and non-native species, could respond differently to management activities (Abella and Covington, 2004; Sutherland and Nelson, 2010; Fiedler et al., 2013). The imprint of major events in forests on understory plant communities can be long-lived, such as persistent effects to plant diversity from Roman clearing of French forests 2000 years ago (Dambrine et al., 2007). Undesirable legacies of forest practices might be avoided if we have a foundation of clear insights on impacts to understory communities.

To help provide such a foundation, systematic reviews are emerging tools for evaluating evidence for ecological questions, including effects of forest management activities (e.g., Rosenvald and Löhmus, 2008; Verschuyt et al., 2011; Duguid and Ashton, 2013). Systematic reviews are complementary to traditional narrative reviews, but differ by having reproducible methods for locating literature, criteria for including or excluding studies, and an evaluation of evidence from reproducibly synthesized primary data (Pullin and Stewart, 2006). Systematic reviews and statistical meta-analyses are not synonymous: data gathered by a systematic review can be analyzed with or without a statistical meta-analysis, and meta-analysis can be applied to numerous data sets other than

those assembled through a systematic review (Koricheva et al., 2013).

Here, we conducted a systematic review of the effects of tree cutting and fire on understory vegetation in mixed conifer forests of interior western North America. Mixed conifer forests are considered among North America's most difficult for fire management, and conservation of these forests is currently of keen interest (Agee, 1993; Klenner et al., 2008; Jain et al., 2012). Contemporary conditions of mixed conifer forests differ from those before or during initial Euro-American settlement (Parsons and DeBenedetti, 1979; Covington et al., 1994; Minnich et al., 1995; Reynolds et al., 2013). Major changes to fire regimes, tree structure and composition, forest floor and light conditions, climate, and introduction of livestock and exotic species may all influence understory vegetation (Battaglia and Shepperd, 2007; Knapp et al., 2013). Except for rare forests such as those with natural fire regimes continued through the 1900s (mostly in Mexico; Minnich et al., 2000) or with managed active fire programs (e.g., Sequoia/Kings Canyon National Parks; Webster and Halpern, 2010), the key evolutionary process of low- and mixed-severity fire has been excluded after settlement (Heinlein et al., 2005; Baker et al., 2007; Falk et al., 2011). Fuel loads accrued during the 1900s support severe, stand-replacing fire regimes in many areas (Freeman et al., 2007; Crotteau et al., 2013; Fornwalt and Kaufmann, 2014). Tree density and basal area have increased on average by orders of magnitude, now often exceeding 1000 trees ha<sup>-1</sup> and 30–80 m<sup>2</sup> ha<sup>-1</sup> basal area (Cocke et al., 2005; North et al., 2007; Fulé et al., 2009). Tree composition has generally shifted toward an increased proportion of species with low fire tolerance and higher shade tolerance, at the expense of fire-tolerant species such as *Pinus ponderosa* (ponderosa pine; Barbour et al., 2002; Vankat, 2011; Abella et al., 2012). Concomitant with increased tree density, light reaching the forest floor has decreased, while O horizons have thickened (Bigelow and North, 2012; Lydersen et al., 2013). Stocking levels of livestock (primarily cattle and sheep) peaked in the mid-1800s or early 1900s among regions, with likely profound but poorly understood impacts (Riggs et al., 2000). A suite of non-native species, ranging from tree pests to plants, can dramatically influence mixed conifer forests at local to regional scales (Hessburg and Agee, 2003).

Associated with these land use and forest structural changes, examples of repeat-photography studies and historical records

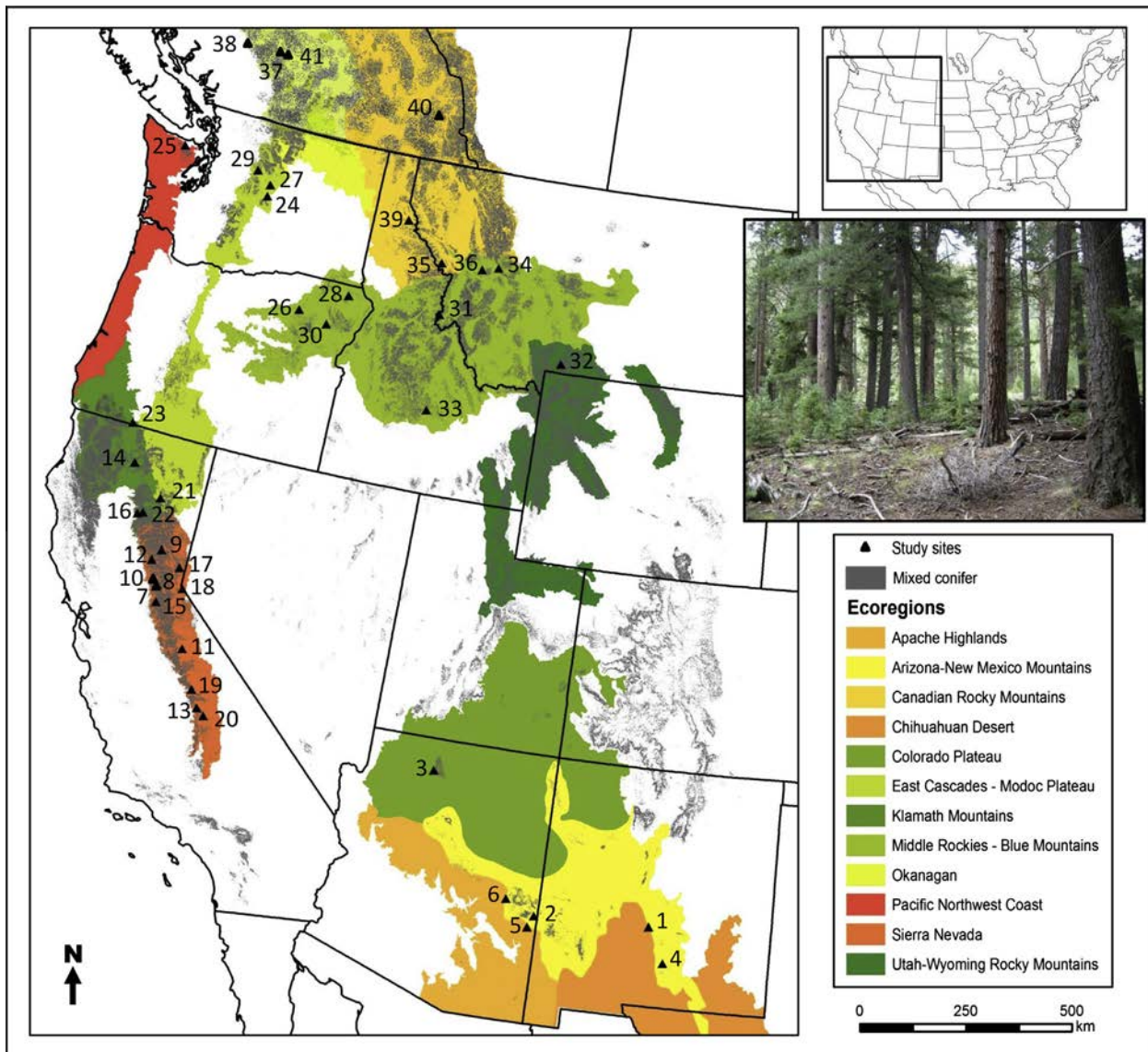
have frequently revealed dramatic changes in understory vegetation since the early Euro-American settlement period. In early settlement photos of Rocky Mountain mixed conifer forests in Idaho and Montana, Gruell (1983) showed examples ~50–100 years later of herbaceous understories of *Lupinus* spp. or *Pseudoroegneria spicata* (bluebunch wheatgrass) largely disappearing under expanded tree canopy; reduced shrub understories such as of *Shepherdia canadensis* (buffaloberry); and shifts in shrub dominance such as to *Cercocarpus ledifolius* (mountain mahogany). Striking aspects of the geographically extensive photos included abundant evidence of disturbance (predominately fire, timber cutting, and livestock) in the late 1800s/early 1900s which related to mosaics of different understories, and numerous pathways of vegetation change in the 1900s, but generally significant expansion of conifer trees and reduced herbaceous plants and shrubs (Gruell, 1983). In analyzing historical inventories from 1897–1902 in California mixed conifer forest reserves, McKelvey and Johnston (1992) concluded that understories were sparse at that time (even though overstories remained open and dominated by large, old trees) owing to drought in the late 1800s, intensive livestock grazing, and severe burning by shepherders. Subsequent exclusion of nearly all fire corresponded with pervasive tree recruitment, resulting in continued limiting of understory plant growth (McKelvey and Johnston, 1992). Overall conclusions from these, and other studies in mixed conifer forests (e.g., Kaufmann et al., 1998; Gruell, 2001; Taylor, 2004), indicate that: (i) understory plant cover has generally decreased during the past ~100 years, likely linked with increased tree density and supported by negative relationships between tree abundance and understory vegetation (Larson and Wolters, 1983); (ii) grazing, fire exclusion, different climatic conditions (from the 1800s to today), and other factors (e.g., air pollution) have likely interacted to change composition or abundance of understory plants in ways not well understood; and (iii) it is difficult to ascertain specific past reference conditions for these understories, suggesting opportunity for developing reference information based on how contemporary vegetation responds to disturbance to help guide future forest management efforts.

The primary question of our systematic review was: How do tree cutting and fire influence understory vegetation in western North American mixed conifer forests? We had five specific questions, each with anticipated outcomes:

- (1) Do tree cutting, managed fire (prescribed or wildland fire use), tree cutting + managed fire, and wildfire have different effects on total understory plant abundance (cover, biomass, density, or other reported measures) and species richness? We anticipated that relative treatment effects would increase in the order: managed fire < cutting < cutting + managed fire < wildfire. Our rationale was that, owing to negative relationships between overstory tree abundance and understory vegetation in undisturbed mixed conifer forests (Larson and Wolters, 1983), treatments should represent a gradient of decreasing overstory correlated with increasing understory vegetation. Note that we purposely refer to wildfire as a ‘treatment’ in this paper, because wildfire often is an eventual ‘de facto’ treatment implemented via passive management in these forests (Stark et al., 2006; Knapp et al., 2012; Crotteau et al., 2013).
- (2) Are understory metrics such as plant cover and species richness related to time since tree cutting or time since fire? We expected that short/moderate time durations after treatment would have the greatest difference with controls, because longer post-treatment durations (decades) could exhibit tree canopy ingrowth or re-accumulation of O horizons (Stephens et al., 2012).
- (3) Do responses to these disturbances vary among plant groups (growth forms and native/non-native species groups)? We anticipated that shrub, forb, and graminoid growth forms overall would respond similarly to treatment, because all these growth forms had evolved in often-disturbed mixed conifer forest and each has mechanisms for persisting in disturbed forest (Bradley et al., 1992). For example, many species of each growth form readily resprout if top-killed and also form soil seed banks to endure through or colonize after disturbance (Abella and Springer, 2012). Although non-native plants do not always require disturbance to become established, disturbance often facilitates their establishment and expansion (McGlone and Egan, 2009). Thus, we evaluated the expectation that non-native plants would exhibit stronger relative responses than native plants to disturbance, at least in the short term.
- (4) Do understory responses to tree cutting and fire differ between moist and dry mixed conifer forest? Relative responses in moist versus dry forest were difficult to forecast, owing to potential counteracting differences between the forest types. For example, dry soil could limit response in dry mixed conifer, yet dense tree canopy from higher tree productivity in moister forest could reduce understories (North et al., 2005), potentially creating similar understory response to treatment between these forest types.
- (5) How do understory responses vary with intensity of tree cutting (e.g., proportion of trees removed) or severity of fire? We forecasted that understory plant measures would increase with intensity of cutting and severity of fire, because overstory limitations imposed on the understory would be alleviated through tree mortality (Fornwalt and Kaufmann, 2014).

## 2. Study area and forest description

Mixed conifer forests frequently occupy elevations between those supporting lower-elevation *P. ponderosa* or *Pinus jeffreyi* (Jeffrey pine) forests and higher-elevation forests such as pure *Abies concolor* (white fir) or subalpine including *Picea-Abies* (spruce-fir) among different regions supporting mixed conifer forests (Battaglia and Shepperd, 2007). Minimum elevation required to support mixed conifer forests generally decreases from southern to northern latitudes (Klenner et al., 2008). Major physiographic regions occupied by mixed conifer forests include the inland Pacific Coast (e.g., Klamath and Sierra Nevada Mountains), Intermountain Region, and Rocky Mountains (Fig. 1). Inland mixed conifer forests occupy parts of northern Mexico, over 17 million ha in the western United States (Schoennagel and Nelson, 2011), and 4 million ha in southwestern Canada (British Columbia Ministry of Forests, 2010). Local topography influences mixed conifer distribution within climate regions and elevation zones, with mixed conifer often inhabiting drainages or north aspects in areas otherwise supporting drier forest. Precipitation in mixed conifer forests usually is about 30–100 cm annually but can exceed 100 cm mainly in the western Sierra Nevada, Klamath, and other mountains closest to the Pacific coast (Appendix A). Snow is common, often providing an important source of early growing season moisture. Summers characteristically are dry, excepting areas receiving late-summer monsoonal storms. Tree species vary by region, with dominants commonly including *P. ponderosa*, *A. concolor*, *Pseudotsuga menziesii* (Douglas-fir), and *Pinus lambertiana* (sugar pine). Historical forest structure generally was characterized by mostly (>50%) open areas without tree canopy and interspersed clumps and individuals of trees (Hagmann et al., 2013; Reynolds et al., 2013). Tree densities historically ranged from ca. tens to hundreds per hectare among regions and sites within regions (North et al., 2007; Fulé et al.,



**Fig. 1.** Distribution of mixed conifer forests in western North America and locations of 41 studies evaluating response of mixed conifer understories to tree cutting or fire. Studies are numbered 1–41 corresponding with Table 1. Mixed conifer distribution adapted from U.S. National Vegetation Classification and ponderosa pine and interior Douglas-fir biogeoclimatic divisions in British Columbia. Ecoregions provided by The Nature Conservancy (Arlington, Virginia). Photo shows mixed conifer forest of *Pinus ponderosa*-*Pinus flexilis*-*Pseudotsuga menziesii* on San Francisco Peaks, near Flagstaff, Arizona (by S.R. Abella, 17 Aug 2008).

2009; Reynolds et al., 2013). Physiognomy of understories currently varies broadly from shrubby, grassy, or forb-dominated, to sparsely vegetated with extensive O horizons (Gruell, 1983; Fites-Kaufman et al., 2007).

Mixed conifer forests are dynamic and shaped by disturbance, with long-term evolutionary development providing a baseline for comparing characteristics of present forest (Covington et al., 1994). Anderson et al. (2008), for instance, reported temporal development of mixed conifer forest in the Jemez Mountains, New Mexico: *Picea parkland* inhabited the area 14,000 years ago after the glacial period, *P. ponderosa* colonized by ca. 11,500 years ago during a warmer climate, and with increased moisture by 6400 years ago, mixed conifer forest arose resembling present tree composition (*P. menziesii*, *A. concolor*, *P. ponderosa*, and others). Charcoal influx sharply increased after 4600 years ago, suggesting a long history of fire, and consistent with a more recent tree-ring-derived fire interval of 35 years from 1624 to 1902

(Anderson et al., 2008). Many mixed-conifer forests sustained fires at least as frequent (often <10-year return intervals) as those in *P. ponderosa* forests, but longer return intervals (including longer than 50 years) could occur in moister forest or where topography limited fire spread, and during climatic periods unfavorable to fire spread. Mixed-severity fire regimes, consisting mostly of low-intensity surface fire punctuated by more severe surface fire or patches of crown fire (Fulé et al., 2003), have been broadly reported in mixed conifer forests from Mexico (Minnich et al., 2000) through the U.S. to Canada (Heyerdahl et al., 2012). Seasonality of fire varied from spring/summer (Fulé et al., 2003) to predominately late summer or fall (Taylor, 2004). In addition to fire, periodic windthrow, insect/disease outbreaks, and extreme climatic events created spatial and temporal heterogeneity via patch creation from individual tree death to larger areas hectares in size (Veblen et al., 2012). These disturbances likely created different biophysical filters to understory vegetation, both within stands and landscapes,

and through time on the same site (Keith et al., 2010; Lydersen et al., 2013).

Few definitions exist of mixed conifer forest (also described as mixed evergreen) in the literature, with one of the few provided by Reynolds et al. (2013) specific to the Southwest: forest occupying elevations between 1525 and 3050 m, sustaining relatively frequent (<35 year fire-return interval) surface fire including some mixed-severity effects, and containing species mixtures of shade-intolerant *P. ponderosa* and shade-tolerant *P. menziesii* or *A. concolor* depending on seral stage. Throughout the range of mixed conifer forest in western North America, tree species present, fire regimes, and elevations inhabited vary among regions (Agee, 1993; Fites-Kaufman et al., 2007; Jain et al., 2012). We define mixed conifer forest as: mixtures of two or more conifer tree species at intermediate elevation (above lower forests such as *P. ponderosa* forest but below higher forests such as *Picea–Abies*) that occupy inland continental locations generally of semi-arid climate in western North America. We consider only stands with two or more conifer species sharing overstory dominance to be mixed conifer, which excludes stands such as pure overstory *P. ponderosa* invaded by other conifers in the understory. In our study, we include both dry and moist mixed conifer, as well as forest with some *Populus tremuloides* (quaking aspen), but not pure *Populus* forest. Reynolds et al. (2013) distinguished dry mixed conifer as having mean fire intervals of <35 years (and >35 years for moist) and occupying south aspects or other dry topographic positions. Dry versus moist types are usually differentiated on a relative basis on regional (e.g., climatically moister versus drier regions) or within-landscape (e.g., opposing north versus south aspects) scales (Jain et al., 2012).

### 3. Methods

#### 3.1. Data collection

We systematically obtained literature addressing our study questions by searching literature databases, screening articles for meeting inclusion criteria, and preparing a database including each study's findings. In April 2014, we searched for articles in the following databases: AGRICOLA, Agris, Academic Search Complete, BioOne, ProQuest (including Biological Sciences, Environmental Science, GeoRef, and Zoological Record), Web of Science, Forest Science Database (CABdirect), Treearch, and Google Scholar. We used the following search words and their combinations for article titles and key words: forest, mixed conifer, coniferous, evergreen, understory, understorey, plants, vegetation, forb, shrub, grass, colonization, indicator species, seed, revegetation, species richness, diversity, regeneration, recruitment, composition, succession, tree, overstory, cutting, felling, thinning, removal, silviculture, shelterwood, harvest, timber, density, fuel, reduction, treatment, management, restoration, burning, fire, and wildfire. We also examined the reference list of each located article for other pertinent articles.

We screened the 128 relevant articles located by this search for their suitability for inclusion in the systematic analysis by requiring that studies meet all of the following criteria. First, studies must be in western North American mixed conifer forest, following our definition. Second, they must present primary, quantitative data on response of an understory species or community to tree cutting or fire. Third, studies must provide a benchmark (pre-treatment condition, untreated/unburned condition, or both) against which to compare effects of tree cutting or fire. By making these relative comparisons of treatment effects within studies, potential differences in vegetation measurement methods, climatic time periods in which data were collected, or other factors that can confound comparisons among studies should be minimized within studies. Fourth, for studies of wildfires, they must also have

included areas not subject to post-fire rehabilitation treatments such as seeding or fertilization. This criterion is important because post-fire treatments can impact species composition by both directly introducing new species and influencing the course of natural recovery (Crane et al., 1983; Peppin et al., 2010). If wildfire studies included areas receiving post-fire rehabilitation treatments and those that did not, we only included data from sites not receiving post-fire treatments. Fifth, studies must be published, either as journal articles, conference proceedings, government serial publications, book chapters, or books.

#### 3.2. Data analysis

We created a database from quantitative results presented for any available understory measure in articles. The main measures presented were plant cover and species richness, but some papers reported biomass, plant density, shrub survival or vigor, and soil seed bank density and species richness. Completeness of vegetation data varied, with some studies providing community composition (species present and their relative abundance) or components of the community (e.g., shrub cover only). Accordingly, we used every study available for each of our study questions independently, with some studies presenting comprehensive community data used for nearly all questions and other studies used only for questions related to specific community components. We calculated a total 'abundance' measure, derived from cover whenever it was presented or from biomass or density, and a 'richness' measure, based on species density per sampling unit. When multi-scale species richness estimates were presented (e.g., species  $m^{-2}$  and species  $1000 m^{-2}$ ), we averaged richness across scales but noted any differences in response to treatment among spatial scales. We used the longest-term data presented in a study, and except for analyses to evaluate treatment intensity or burn severity, we averaged data across different intensities of a treatment type (e.g., different levels of thinning) in the infrequent cases where different intensities were presented.

From extracted data for both understory abundance and richness, we calculated a ratio of treatment:control or after:before treatment. For studies with both pre-treatment data and controls, we first calculated the after:before ratio then used that to calculate the treatment:control ratio. Some papers presented data as relative differences (such as percent change from pre- to post-treatment), which could result in negative ratios. Additionally, some studies had zeros as denominators (e.g., if controls had zero plants), precluding calculation of ratios. In these cases, we simply calculated the raw difference between after/before or treated/control values.

We considered conducting a formal statistical meta-analysis, but the available data had several features that limited meta-analysis. Presentation of relative differences (resulting in negative values) or presence of zeros in some studies, together with many papers not reporting a measure of variability or being unreplicated, complicated calculation of meta-analytical statistics (Harrison, 2011). It is noteworthy, but not uncommon, that some of the most ecologically insightful studies in our data set did not meet requirements for calculation of standard meta-analysis statistics, such as Knapp et al.'s (2013) remeasurement of 79-year-old silvicultural treatments installed in 1929. Another significant issue was that, for several of our questions, approximately equal proportions of decreases and increases were reported across studies. Analyzing an average or median effect size in this situation represented an effect size (i.e., zero or no change) rarely or never actually occurring in the literature.

We adopted a hybrid approach to data analysis by using a combination of effect sizes (after:before or treatment:control ratios) as appropriate, ranking relative responses to treatments, and categorizing understory responses to treatment as relative

**Table 1**  
Summary of 41 studies examining effects of tree cutting, prescribed fire, or wildfire in mixed conifer forests of western North America. Studies are organized by general region from south to north. For studies reporting a measure of total plant abundance (e.g., cover, biomass) and total species richness, relative magnitude of response to treatments is provided.

Reference	Treatments <sup>b</sup>	Years post-tmt	Plant abundance <sup>c</sup>				Species richness <sup>c</sup>				Data extracted <sup>d</sup>	Map No. <sup>e</sup>
			C	PF	C+PF	W	C	PF	C+PF	W		
<i>Southwest</i>												
Cram et al. (2007)	T	0.5	–								GF cv	1
Ffolliott and Gottfried (1989)	Patch cutting	8	+								Herb biomass	2
Huisinga et al. (2005)	PF	6		+				+			CC	3
Mason et al. (2009)	T	2–3	+				+				GF cv, sr	4
Patton (1976)	Patch cutting	2	+								GF biomass	5
Thill et al. (1983)	T, patch cutting	4 (T), 16 (patch)	+								Biomass	6
<i>Sierra Nevada</i>												
Battles et al. (2001)	S, single tree	19	+					+			GF cv, sr	7
Bêche et al. (2005)	PF	0.5		–				–			cv, sr	8
Chiono et al. (2012)	T with PF	2–15									Shrub cv	9
Collins et al. (2007) <sup>a</sup>	T, PF, T+PF	1–2	–	+	–		–	–	–	–	GF cv, sr	10
Hurteau and North (2008)	PF	1		–				–			GF cv, sr	11
Kauffman and Martin (1990)	PF	2									Shrub survival	12
Knapp et al. (2007)	PF	2		+				+			CC	13
Knapp et al. (2012)	PF, wildfire	4 (PF), 15 (W)									Shrub cv, sb	14
Knapp et al. (2013)	T, selection cutting	79									Herb sr, shrub cv	15
Siegel and DeSante (2003)	T	5–8	+								cv	16
Walker et al. (2012)	T, PF, T+PF	4	+	–	–						cv, biomass	17
Walker et al. (2013)	Wildfire	4						–			GF cv, biomass	18
Wayman and North (2007)	T, PF, T+PF	3	–	–	+		++	+	+++		GF cv, sr	19
Webster and Halpern (2010)	1st, 2nd entry PF	20		+				+			GF cv, sr	20
Zhang et al. (2008)	T with PF	5									Shrub cv, sr	21
<i>California Cascades/Klamaths</i>												
Crotteau et al. (2013)	Wildfire	10									Shrub cv, sr	22
Donato et al. (2009)	Wildfire	2					+			+	CC	23
<i>Northwest</i>												
Dodson et al. (2008) <sup>a</sup>	T, PF, T+PF	1–3	–	+	–		–	+	++		GF cv, sr, biomass	24
Fonda and Binney (2011)	PF	3		–							cv	25
Hardman and McCune (2010)	T with PF	3–4									Shrub cv	26
Harrod and Halpern (2009)	PF	2									Survival 2 rare spp	27
Metlen et al. (2004) <sup>a</sup>	T, PF, T+PF	1–6	–	–	–	–	–	–	–		CC	28
Scherer et al. (2000)	CL, CL with PF	2					–		+		cv, sr	29
Young et al. (1967), Hedrick et al. (1968)	Sanitation cutting	3–4	–								GF biomass	30
<i>Central Rockies</i>												
Ayers et al. (1999), Bedunah et al. (1999)	S, S+PF	1									Shrub density	31
Gordon (1976)	PF	2									Shrub density	32
Lyon (1966)	PF	2						–			GF density, sr	33
Metlen and Fiedler (2006) <sup>a</sup>	T, PF, T+PF	3	–	–	–	–	+	–	++		CC	34
Newland and DeLuca (2000)	PF, wildfire	9									N-fixing plant cv	35
Steele and Beaufait (1969)	CL, CL with PF	1	–		–		+		–		cv, sr	36
<i>Interior British Columbia</i>												
Ducherer et al. (2009)	PF	3		+				–			CC	37
Ducherer et al. (2013)	T	4	+					–			CC	38
Lochhead and Comeau (2012)	Selection cutting	15	+								GF cv	39
Page et al. (2005)	T	1									Herb cover	40
Stark et al. (2006, 2008)	CL, wildfire	1	–				–	–		–	sb density and sr	41

<sup>a</sup> Fire and Fire Surrogate study sites with complete listing of understory papers from which data were extracted: Blodgett, Collins et al. (2007); Mission Creek, Dodson et al. (2008), Dodson and Peterson (2010), Agee and Lolley (2006); Blue Mountains, Metlen et al. (2004), Youngblood et al. (2006); Lubrecht, Metlen and Fiedler (2006), Dodson and Fiedler (2006), Dodson et al. (2007), Gundale et al. (2006).

<sup>b</sup> CL, clearcutting; PF, prescribed fire; S, shelterwood; T, thinning.

<sup>c</sup> Plant abundance and richness are for studies that measured the complete vascular plant community (i.e. excludes studies that did not measure all vascular plant growth forms). Treatments are abbreviated as: C, cutting (includes any type of cutting such as thinning, shelterwood, and patch cutting); PF, prescribed fire; and W, wildfire. Response is categorized as decrease (–, ––, or –), proportional to magnitude of decrease across treatments within a study, or as [–] for studies with only one treatment, or increase (same notation, where +++ indicates the greatest increase). For richness in Metlen et al. (2004), there was a tie, so two treatments were assigned [–].

<sup>d</sup> CC (community composition, which includes species present and a measure of their relative abundance), GF (data provided by growth form), cv (cover), sr (species richness, and in rare cases a diversity index), and sb (seed bank).

<sup>e</sup> Study location in Fig. 1.

increase (ratios >1, or raw difference >0), no change (ratios = 1 or difference = 0), or decrease (ratios <1, difference <0). For Question 1 (relative influences of treatments on total understory plant abundance and species richness), we ranked relative responses of an understory measure among treatments within a study (e.g., +++ signified the greatest increase among treatments in a study where an understory measure increased in all three treatments) and as increase (+) or decrease (–) if only one treatment was evaluated

in a study. For Question 2 (influence of time since treatment), we regressed time since treatment with treatment : control ratio of total plant abundance and species richness. For Question 3 (responses among plant groups), we categorized responses of growth forms (shrub, forb, graminoid) as increase or decrease to each treatment type ('no change' did not occur). We compiled relative responses to treatment (in the same way as for Question 1) of non-native plants, because most studies that evaluated

non-natives applied treatments factorially to enable relative ranking. No studies were identified that evaluated Question 4 (treatment effects in moist versus dry mixed conifer), but we did assess potential relationships between long-term average precipitation of a study area and understory response to treatment for studies that provided precipitation data. For Question 5 (influence of treatment intensity or fire severity), we calculated the number of studies in which the greatest response to treatment was in high or low treatment intensity or burn severity. We designated the cutting treatment that removed the most tree basal area to be most intensive, and we used the classification of severity presented in papers for managed fires (hereafter referred to as prescribed, because no wildland fire use fires were reported) and wildfires (if low, moderate, and high severity were all presented, we used low and high). We summarized quality of evidence for each study by tabulating metrics of study design (collection of pre-treatment data, inclusion of unmanipulated controls, site replication, and replication across some type of environmental gradient such as soil parent material or burn severity for wildfire) and duration of data collection after treatment.

## 4. Results

### 4.1. Description of the literature

The systematic literature search identified 41 published studies, reported in 50 articles (some studies were reported in >1 article), which met inclusion criteria for quantitatively evaluating influences of tree cutting and fire on understory vegetation in western mixed conifer forests (Table 1). Most articles were published recently: 78% (39 of 50 articles) in the 2000s, 6% (3 articles) in the 1990s, 4% (2 articles) each in the 1980s and 1970s, and 8% (4 articles) in the 1960s. Four studies, reported in 10 articles, were from four of the network of sites in the U.S. Fire and Fire Surrogate Study initiated in the early and mid-2000s (Table 1).

Studies covered a broad geographic area, being conducted in one Canadian province (British Columbia, 5 studies, 12% of 41 studies) and seven states in the U.S.: Arizona (4 studies, 10%), New Mexico (2, 5%), California (16, 39%), Oregon (4, 10%), Washington (4, 10%), Montana (5, 12%), and Idaho (1, 2%). No studies were identified from Mexico, although mixed conifer forests occur there. Regions in which several studies were conducted included the Colorado Plateau in the Southwest, Sierra Nevada Mountains, Cascade Mountains, Blue Mountains, northern Rocky Mountains, and interior British Columbia. Estimates of annual precipitation in study areas were provided for 79% of studies and were commonly ~40–80 cm yr<sup>-1</sup>, with some study areas inland, but nearest the coast, reporting >100 cm yr<sup>-1</sup> of precipitation (Appendix A). Species richness and identity of dominant tree species were diverse among studies. Overstory dominants commonly included *P. ponderosa*, *Pseudotsuga menziesii*, *A. concolor*, *P. jeffreyi*, *P. lambertiana*, *Calocedrus decurrens* (incense cedar), *Picea engelmannii* (Engelmann spruce), and nine others. About half (43%) of studies reported average fire intervals for their study areas before fire exclusion in ~1900. Fire was common in study areas, with intervals often <10 years and usually <30 years. Longer intervals averaging ~40–75 years were reported in some study areas.

Dominant understory growth form (shrub, forb, graminoid, or forbs and graminoids combined into an herbaceous category), in the pre-treatment or control plant community, was identified in 46% of studies by providing cover or biomass across growth forms. Seven (37%) of these 19 studies reported that shrubs were most dominant, 11 (58%) that herbaceous understories predominated, and 1 (5%) study reported equal shrub and herbaceous abundance.

Appendix B provides photographs from a range of studies illustrating understory condition.

Treatments evaluated were diverse and implemented for numerous objectives, such as patch cutting to create openings for wildlife (Patton, 1976), silvicultural improvement (e.g., Knapp et al., 2013), timber harvest (e.g., Steele and Beaufait, 1969), restoration of frequent fire in a national park context (Webster and Halpern, 2010), and hazardous fuel reduction (e.g., Mason et al., 2009; Chiono et al., 2012). Twelve studies (29%) examined some variation alone of tree cutting (e.g., patch cutting, tree thinning), 13 (31%) examined prescribed fire alone, 10 (24%) evaluated composite or factorially applied cut + burn treatments, and 6 (14%) studies included wildfires.

### 4.2. Study designs and quality of evidence

Nearly half (43%) of studies had both pre-treatment data and controls, with about the same percentage having only controls and the remainder before/after designs (Appendix A). Most studies (71%) included replicated treated sites. No study replicated sites across any type of stratified environmental gradient such as elevation or soil parent material, but three studies of wildfires stratified by burn severity (Stark et al., 2006; Donato et al., 2009; Crotteau et al., 2013). The time since treatment that measurements were made ranged from <1 year to ≥10 years (Thill et al., 1983; Chiono et al., 2012; Lochhead and Comeau, 2012; Crotteau et al., 2013), including the longest-term studies of 19 (Battles et al., 2001), 20 (Webster and Halpern, 2010), and 79 (Knapp et al., 2013) years after treatment. Most studies (63%) were of short duration, measuring response a maximum of three years post-treatment.

### 4.3. Evidence for responses to treatments

#### 4.3.1. Question 1 (relative influences of treatments on total understory plant abundance and species richness)

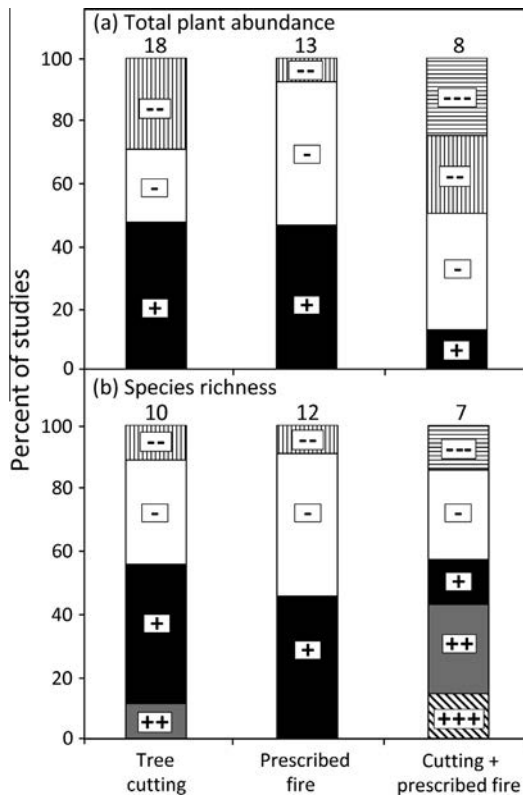
Cutting and prescribed fire applied individually similarly increased understory plant abundance (usually measured as cover) or species richness in about half of studies (Fig. 2). Applying cutting and prescribed fire together typically resulted in decreased plant abundance, but increased species richness.

#### 4.3.2. Question 2 (influence of time since treatment)

The longest-term studies usually found increases in total understory plant measures after cutting or prescribed fire (Fig. 3). The five longest-term (8 to 19 years after treatment) studies of cutting (that included total plant measures) all reported increases in total plant abundance, and seven of the eight studies (87%) ≥4 years in duration found increases. In comparison, only 2 of 10 studies (20%) with durations <4 years reported increases. For prescribed fire, the two longest-term studies (6 and 20 years) reported the greatest increase in total plant abundance. There were fewer data points for cutting and prescribed fire applied together, and no study exceeded 4 years in duration.

Species richness was measured in fewer long-term cutting studies than was plant abundance, but the greatest relative increase also was reported in the longest-term study of 19 years (Fig. 3). Although the two longest-term (6 and 20 years) studies of prescribed fire reported the 2nd and 3rd greatest increase in richness, the greatest increase occurred in a study two years post-fire. Nevertheless, only a third of nine studies ≤4 years in duration reported increased richness. After cutting + prescribed fire, the two shortest-term studies (both of 1 year) both reported declines in richness, whereas four of five studies of ≥2 years reported increases.

Other long-term studies evaluating specific components of the plant community illustrated post-treatment dynamics. Chiono



**Fig. 2.** Response of total understory plant abundance (cover, biomass, or density) and species richness among treatments in mixed conifer forests of western North America. Magnitude of response is categorized relative to treatments compared within studies (e.g., +++ signifies the greatest increase within a study that included the three treatments of cutting, fire, and their combination) or as increase (+) or decrease (–) in studies including one treatment. Number of studies is given at the top of bars.

et al. (2012) found that the oldest fuel treatments (cut + prescribed fire) 8–15 years old exhibited the highest shrub cover (16%) relative to controls (7%), compared to younger treatments 2–7 years old in the Sierra Nevada Mountains. Knapp et al. (2013) reported that shrub cover was reduced from 29% before selection cutting in 1929 to 15% after treatment, rebounded to near pre-treatment levels by two years after treatment in 1931, and declined to 3% at 79 years after cutting in 2008. Similarly, herbaceous species richness averaged 1.5 species/4 m<sup>2</sup> in 1929 before cutting, declined to 1.0 species later that summer after cutting but doubled two years after cutting, and again declined to 1.0 species/4 m<sup>2</sup> in 2008. Tree density by 2008 was more than twice that (739 compared to 315 trees ha<sup>-1</sup>) before cutting in 1929, and repeat photographs depicted a shift from forest floors dominated by shrub cover to thick O horizons (Appendix B5). Ten years after wildfire, Crotteau et al. (2013) reported that shrub cover was 2–8 times greater across burn severities compared to unburned forest. Similarly, Lochhead and Comeau (2012) found that graminoid and shrub cover were about 1.4 times greater than controls at 15 years after selective cutting in British Columbia. Collectively, results of these studies supported those of the long-term studies evaluating total community measures in finding that understory measures were increased on older treatments, though Knapp et al. (2013) suggested limits to treatment longevity associated with tree canopy infilling.

#### 4.3.3. Question 3 (responses among plant groups)

Forbs and graminoids increased more frequently in abundance than did shrubs across cutting, prescribed fire, and combined

cutting + fire treatments (Fig. 4a–c). Shrub abundance usually decreased after treatments, a trend particularly evident after combined cutting + fire, where seven of eight (13%) studies reported that shrubs declined. Fewer studies measured species richness than measured cover, and no conclusive trends in richness emerged, except that forb richness may increase more frequently after treatment than other plant groups. Results were mixed after wildfires: half of studies reported decreases in shrub cover while half reported increases (Fig. 4d).

Frequency and magnitude of increase in non-native plant abundance (which was exclusively reported as cover) was least after cutting, intermediate after prescribed fire, and greatest after cutting + prescribed fire (Fig. 5). Non-native species richness increased after all treatments, and most vigorously when cutting and prescribed fire were both applied, in all studies measuring non-native richness. Despite these increases, non-natives comprised only small portions of total plant cover and richness. For example, non-native cover six years after prescribed fire was 1% (compared to 49% native) in mixed conifer forest in Grand Canyon National Park of Arizona (Huisinga et al., 2005), also 1% (compared to 12% native) one year after cutting + prescribed fire in the Sierra Nevada Mountains of California (Collins et al., 2007), and 10% (compared to 58% native and 4% non-native cover in the control) three years after cutting + fire in the University of Montana Lubrecht Experimental Forest (Dodson and Fiedler, 2006). Thus, native species largely constituted the total plant abundance and richness measures and corresponding responses to treatments (Fig. 2). It is noteworthy that few non-native plant data are available for wildfire to compare with cutting and prescribed fire.

#### 4.3.4. Question 4 (treatment effects in moist versus dry mixed conifer)

No studies compared response to treatment between moist and dry mixed conifer forest. Effect sizes for total plant abundance after cutting ( $r^2 = 0.04$ ,  $n = 18$ ) and prescribed fire ( $r^2 = 0.01$ ,  $n = 13$ ) were not closely related to average long-term precipitation in study areas, indicating little relationship between response to treatment and average precipitation in this data set. Similarly, there was little relationship between effect sizes for species richness and average long-term precipitation of study areas for cutting ( $r^2 = 0.11$ ,  $n = 10$ ) or prescribed fire ( $r^2 = 0.00$ ,  $n = 12$ ).

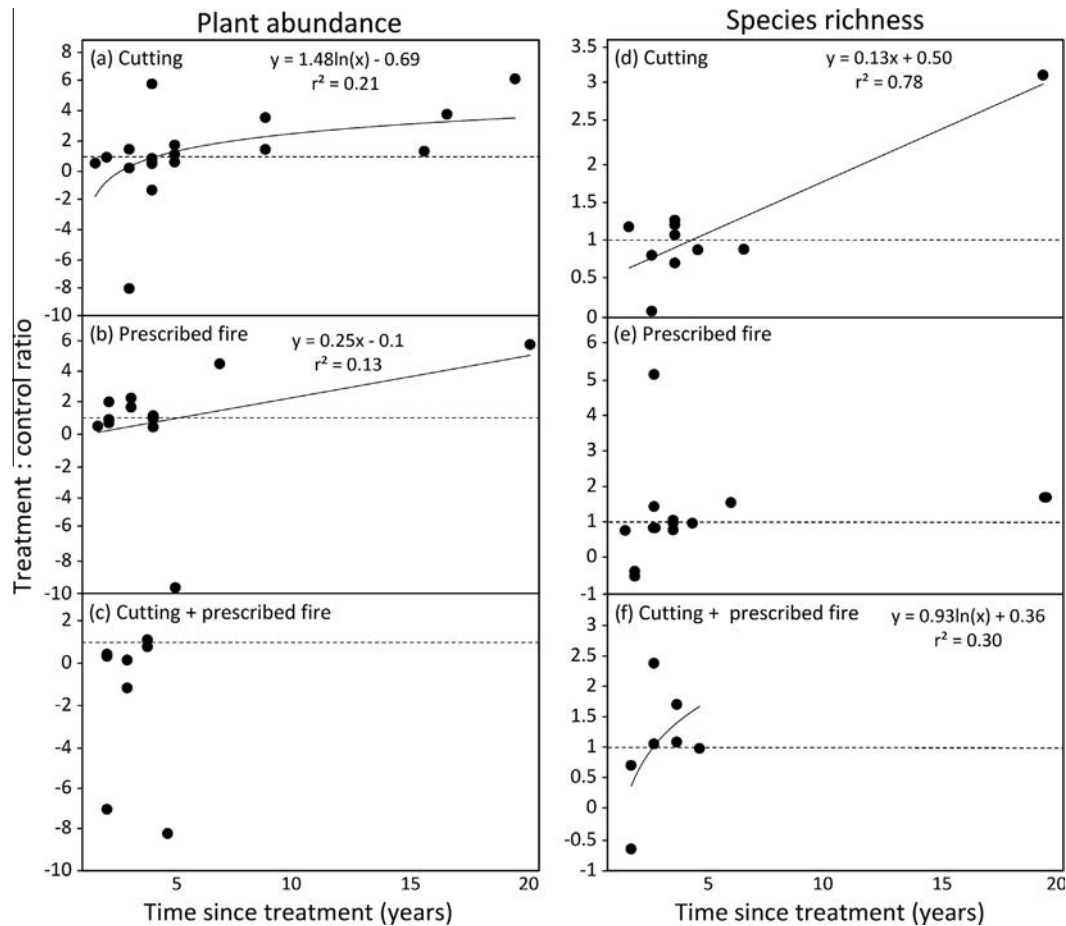
#### 4.3.5. Question 5 (influence of treatment intensity or fire severity)

Results were mixed for the few studies comparing cutting intensity (Fig. 6). For prescribed fire and wildfire, high-severity burning generally (4 of 5 studies) displayed greater increase in total plant abundance and richness than did low-severity burning.

## 5. Discussion

Consistency of available evidence with our *a priori* expectations varied among our five specific questions and among understory metrics. Increasing plant abundance did not occur along the expected gradient of prescribed fire < cutting < cutting + prescribed fire (less information was available for wildfire). About the same proportion of cutting and prescribed fire studies reported increases, and cutting + fire together usually resulted in decreases, but as will be discussed, these were short-term results. Cutting + prescribed fire did induce the largest increase in species richness, but increases occurred less frequently after prescribed fire alone than after cutting alone. Time since treatment was related to understory response, but contrary to our expectation, the longest-term studies reported the greatest increases, with the exception of a 79-year study likely exceeding treatment longevity in the absence of fire (Knapp et al., 2013). Although each plant growth form did exhibit both increases and decreases to





**Fig. 3.** Relationship between time since treatment and response of total understory plant abundance (cover, biomass, or density) and species richness among treatments in mixed conifer forests of western North America. Treatment : control ratios exceeding 1.0 (above broken horizontal lines) indicate that treatments increased understory measures. Note how the longest-term studies, exceeding 6 years post-treatment, usually found that treatments increased understory measures. Coefficients of determination ( $r^2$ ) are given when they exceeded 0.10 (note for [d], the high  $r^2$  largely results from the single long-term study).

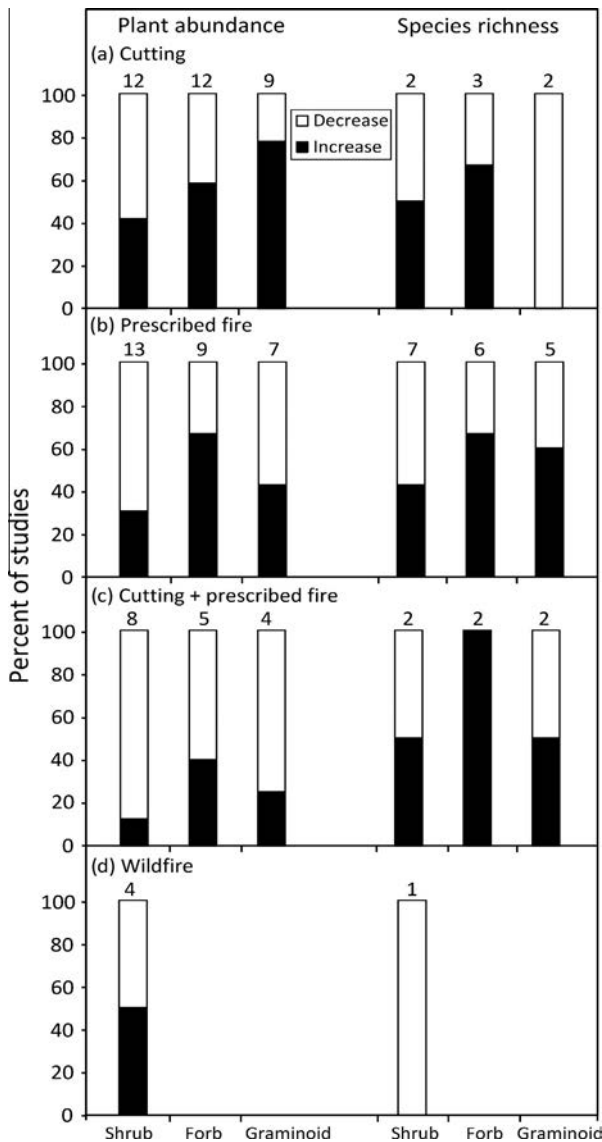
treatments among studies, forbs and graminoids most often increased compared to shrubs. This differed from our expectation of similar responses among growth forms, although variability among studies was high. Consistent with our expectation, non-native plants increased more frequently after treatment than did natives, but it is noteworthy that non-native plants were sparse after treatments compared to native species. Insufficient evidence existed to compare response of moist and dry mixed conifer understories. Few studies compared intensities of cutting or severities of fire, and results were mixed for response of plant abundance to cutting, but increases were generally greatest after higher severity than lower severity fire.

In interpreting findings, some key points explored in the following sections include short- versus long-term dynamics in post-treatment understories; factors such as amount of tree canopy cover removed, treatment implementation operations, slash, and grazing potentially influencing understory response in both the short and long term; a possible tradeoff in short-term decrease of understory abundance (total community cover or biomass) with enhancements of disturbance-promoted native species; condition of the pre-treatment plant community (including soil seed banks) and often a century of fire exclusion as a factor in post-treatment response; and treatment strategies requiring further experimentation, such as delaying prescribed fire following tree cutting. It is also noteworthy that none of the 41 studies had a goal to 'restore the understory'. Rather, project goals included reducing fuels, meeting silvicultural objectives (e.g., timber harvest, sanitation

cuts), or promoting forage availability to livestock and wildlife. Thus, a potential criticism of the studies – that reference conditions (before disruption of disturbance regimes beginning in the middle-1800s) for understories of mixed conifer forests are poorly understood – is not applicable, because study goals were to assess effects of manipulating tree structure and fire on understory vegetation and not to 'restore' the understory. Even when tree cutting or fire reduced total understory abundance in the short term, there was no evidence that these treatments eliminated species within study areas. On the contrary, there was evidence that treatments minimally influenced or increased native species uncommon in untreated forests, including some state-listed endemic species (Harrod and Halpern, 2009), and all 7 long-term studies exceeding 5 years post-treatment reported increases in total plant abundance and species richness. Collectively, published literature suggests a model of understory response to cutting and fire that often includes short-term declines but long-term increases, and particular benefits to disturbance-promoted native understory species. It is possible that these species had been reduced by fire exclusion and concurrent tree canopy closure during the past century.

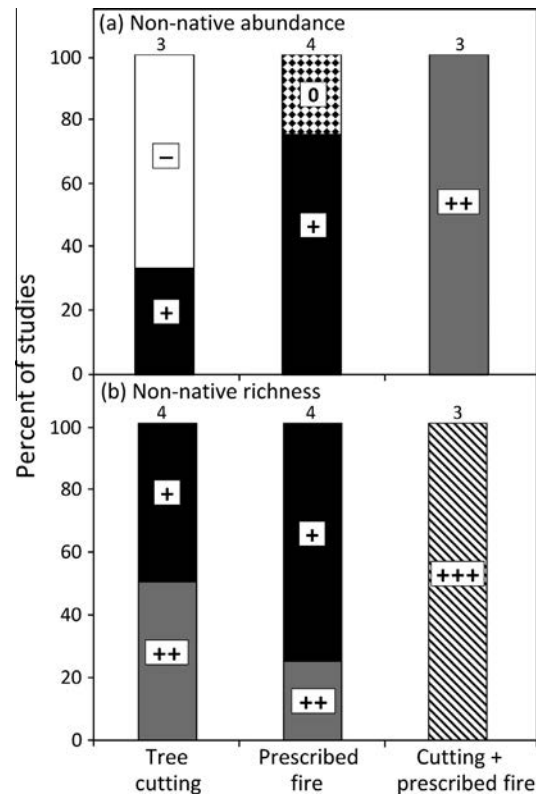
### 5.1. Time since treatment and long-term studies

Declines in understory vegetation (especially in abundance) relative to pre-treatment or controls were commonly reported for the first few years after treatment, but most longer term studies exceeding 4 years after treatment reported increases in understory



**Fig. 4.** Response of plant abundance (cover, biomass, or density; left column) and species richness (right column) by growth form as increase or decrease to treatment among studies in mixed conifer forests of western North America. Number of studies is given at the top of bars.

vegetation. In examining the 7 longest-term studies which all found increases in plant cover or richness, the studies included 5 cutting and 2 prescribed fire studies, were widely distributed geographically from the Southwest to British Columbia, and included several different assemblages of overstory trees and understories dominated by shrubs or herbaceous vegetation. In addition to being long term, the main commonality among these studies was that substantial reduction in overstory tree abundance was achieved and the reduction persisted. Two cutting studies in Arizona had no residual trees in patch cuts up to 1 ha in size (Patton, 1976; Ffolliott and Gottfried, 1989), and Huisinga et al. (2005), also in Arizona, had 30% tree canopy cover after prescribed fire compared to 63% in unburned areas. Nineteen years after a shelterwood cut in the Sierra Nevada Mountains in California, basal area was  $10 \text{ m}^2 \text{ ha}^{-1}$  compared to  $80 \text{ m}^2 \text{ ha}^{-1}$  in controls (Battles et al., 2001). Also in the Sierra Nevada, Webster and Halpern (2010) found that prescribed fire reduced tree density by 60%, and density in burned areas remained proportionally lower than unburned areas for their 20-year study. Similarly, density was



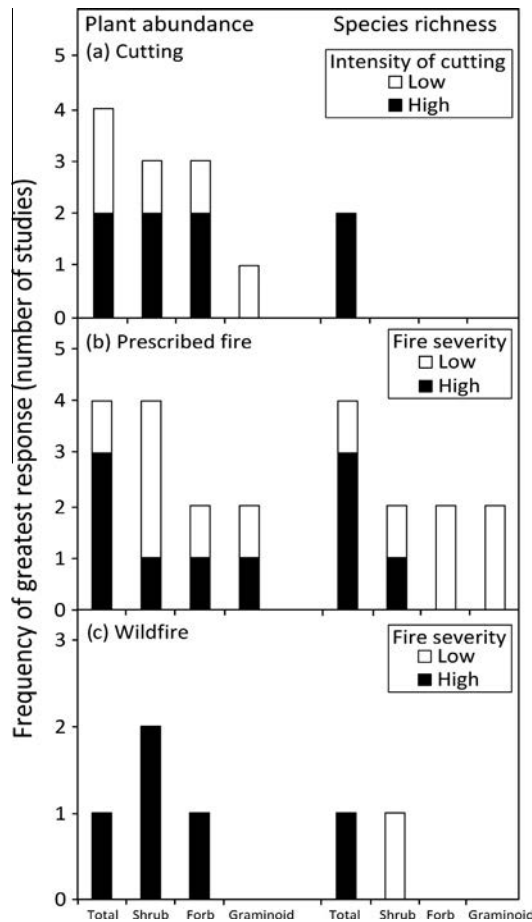
**Fig. 5.** Response of non-native plant abundance (cover) and species richness among treatments in mixed conifer forests of western North America. Magnitude of response is categorized relative to treatments within studies (e.g., +++ signifies the greatest increase within a study that included the three treatments of cutting, fire, and their combination) or as increase (+) or decrease (-) in studies including one treatment. There was no change (signified by a zero) in exotic plant abundance after prescribed fire in one study (Collins et al., 2007). Number of studies is given at the top of bars.

reduced by 56% in Siegel and DeSante (2003) in the Sierra Nevada, and basal area by 33% in Lochhead and Comeau (2012) in British Columbia 15 years after selection cutting.

Annual variation in weather during post-treatment periods could influence response to treatment in both the short and long term, but this is difficult to evaluate because few studies exceeding four years in duration measured multiple post-treatment years. Webster and Halpern (2010) was one of the few studies to do so, finding that cover increased slightly 2 and 5 years after prescribed burning but did not differ significantly from controls until 10 years post-fire. The years post-fire corresponded with different calendar years depending on when different sites were burned, complicating relating vegetation dynamics with weather patterns. Other long-term studies gathered post-treatment measurements in years of below average (Huisinga et al., 2005) or near average precipitation (Thill et al., 1983).

## 5.2. Short-term declines: importance of time, overstory, slash, plant damage, and herbivory

Numerous factors could relate to why most short-term (<4 years) studies found declines in understory plant abundance after treatments. In the two shortest-term studies of 0.5 years, for example, cutting or prescribed fire was implemented in fall and the post-treatment measurement occurred the following spring or early summer, so warm-season plants in particular may not have had opportunity to initiate growth (Bêche et al., 2005; Cram et al., 2007). It should be noted, however, that primary goals



**Fig. 6.** Response of total understory plant abundance (cover, biomass, or density; left column) and species richness (right column) to intensity of tree cutting (high signifies greatest overstory reduction) or severity of fire in mixed conifer forests of western North America. For example, for (a), two studies found that shrub abundance was highest in the most intensive cutting treatment, while one study found that shrub abundance was highest in a low-intensity cutting treatment.

of these studies were to evaluate short-term treatment effects on stream chemistry (Bêche et al., 2005) or soil erosion (Cram et al., 2007), not on understory vegetation. Moreover, temporal photos in follow-up by Cram et al. (2007) suggested increasing amounts of understory cover (Appendix B1).

Treatments that do not appreciably reduce overstory tree canopy cover may not substantially change the understory. The four fire and fire surrogate studies – all of which reported short-term declines in understory abundance – noted that reductions in overstory cover were often relatively subtle, post-treatment overstory cover was likely greater than in historical forests, and relatively dense post-treatment overstories may have limited understory growth (e.g., Metlen et al., 2004; Dodson et al., 2008). Prescriptions were not tailored specifically to promote understories, as the primary objective of these studies was to modify fuel conditions such that 80% of dominant or co-dominant trees in the post-treatment forest would survive wildfire modeled under 80th percentile weather conditions (McIver et al., 2013). Some authors of other studies, such as Mason et al. (2009), also suspected that minimal treatment effects on the overstory tempered understory response within one or more of their treatment units.

Relationships depicted in regression equations between overstory tree abundance and understory measures in untreated mixed conifer forests may provide a framework for estimating overstory reductions needed to stimulate understory vegetation (Larson

and Wolters, 1983; Page et al., 2005). For example, in Rocky Mountain mixed conifer forests of Colorado, Mitchell and Bartling (1991) reported that understory biomass averaged  $535 \text{ g m}^{-2}$  when tree canopy cover was 11–40%, but when tree cover exceeded 60%, understory biomass was reduced by 84% to only  $86 \text{ g m}^{-2}$ . In Idaho *Abies grandis* (grand fir)–*P. menziesii* forest, understory biomass exceeded  $1000 \text{ kg ha}^{-1}$  only up to 40% tree canopy cover (Pyke and Zamora, 1982). Similarly, Hedrick et al. (1968) found that understory production was lowered by over half when tree canopy cover exceeded 40% in the Blue Mountains of Oregon. A doubling of tree basal area from  $11.5 \text{ m}^2 \text{ ha}^{-1}$  to  $23 \text{ m}^2 \text{ ha}^{-1}$  also approximately halved understory biomass in the White Mountains of Arizona (Thill et al., 1983). While specific quantities vary among regions and likely with soil properties within regions, <40–50% tree canopy cover is apparently a threshold above which understory production is minimal. Moreover, treatments need to reduce tree cover down to roughly 20–30% to achieve vigorous understory production based on these overstory-understory relationships (Larson and Wolters, 1983). Similarly, reductions in basal area down to  $<20 \text{ m}^2 \text{ ha}^{-1}$ , and commonly  $8\text{--}15 \text{ m}^2 \text{ ha}^{-1}$ , are apparently approximate thresholds for understory abundance (Thill et al., 1983; Battles et al., 2001; Lochhead and Comeau, 2012).

Residual slash following tree cutting may play a major, but poorly understood, role in post-treatment understory dynamics. Slash can decrease understory vegetation by burying plants (Metlen et al., 2004), or through other mechanisms such as immobilization of soil nutrients in carbon-enriched soil (Perry et al., 2010). These negative impacts, at least at the heavy loadings of slash resulting from contemporary densely treed forests, apparently outweigh any positive effects like creation of shaded microsites. Slash can persist for some time: Munger and Westveld (1931) noted that slash scattered in Oregon dry conifer forest remained largely intact for 7 years and partially broke up by 15 years, with piled slash largely intact longer than 15 years. How slash was handled was not always specified in papers of our systematic review, and methods of treating slash rarely tested. At least five studies scattered slash (e.g., Metlen et al., 2004; Metlen and Fiedler, 2006; Collins et al., 2007; Cram et al., 2007; Dodson et al., 2008) and others moved it off site (Ffolliott and Gottfried, 1989). Among studies examining slash handling methods, Mason et al. (2009) found that piling slash correlated with lower site-level understory biomass than did scattering slash. Two studies found that burning slash (either scattered, Steele and Beaufait (1969), or chipped slash, Walker et al. (2012)) reduced plant cover more than simply leaving the scattered or chipped slash.

Studies focused on effects of slash on understory vegetation in other western forests have mainly reported that slash negatively impacts understories and provide comparisons of treatment options that may be applicable to mixed conifer forests. In thinned New Mexico pinyon-juniper woodlands, Brockway et al. (2002) reported that plant abundance was greatest when slash was moved off site, compared to scattering slash or leaving it around cut trees. Similarly, in thinned Sierra Nevada *P. ponderosa* forest, Kane et al. (2010) found that plant cover increased most after removing slash compared to mastication or mastication + fire. In Arizona *P. ponderosa* (Korb et al., 2004) and Colorado *Pinus contorta* (lodgepole pine) forest (Fornwalt and Rhoades, 2011), burning piled slash sterilized soil and essentially eliminated plant cover in areas that had been underneath piles. Collectively, these observations suggest that slash (and associated slash treatments) can temper understory response to tree cutting and may be related to reductions in understory vegetation reported in some short-term studies of this review. While in some cases it may be practical to move slash off site, such as moving slash to cover decommissioned roads or skid trails, transporting slash off site is usually impractical, necessitating that slash be left or treated on site (Jones, 1974). Deciding

whether to leave slash untreated on site, or to choose among candidate treatments for slash (e.g., broadcast burning, pile burning, mastication), represents tradeoffs among balancing fire hazard, economic costs, limiting insect/disease potential that can be exacerbated through concentrating dead wood, and aesthetics (Seidel and Cochran, 1981; Kreye et al., 2014). Further research that compares influences of slash treatment methods on vegetation in the short and long term in mixed conifer forest is warranted.

Tree cutting operations and fire can damage or kill plants, requiring time for them to recover, especially in the short growing season typifying mixed conifer forests (Metlen et al., 2004). Depending on how and when (e.g., summer versus over snow cover) tree cutting operations are implemented, soil disturbance can be substantial. Young et al. (1967) reported that 39% of the ground was disturbed in some way by a sanitation cut, and 62% was disturbed on steep slopes when thinning trees using heavy machinery (Cram et al., 2007). Machinery, as well as felling trees by hand coupled with slash treatments, can damage or kill aboveground plant parts or disturb root systems belowground (Page-Dumroese et al., 1991). Similarly, fire can damage or kill plants, especially if they are a primary fuel (Kauffman and Martin, 1990). Bedunah et al. (1999), for example, reported that 62% of *Purshia tridentata* (antelope bitterbrush) shrubs were killed by even low-severity fire in a Montana mixed conifer forest. If extant vegetation, including root systems, is appreciably damaged by treatment operations and without rapid recruitment from soil seed banks or off-site seed sources, reduced understory vegetation for one or more growing seasons following treatment may not be surprising.

Based on the few studies that examined herbivory after treatment, combined with herbivory exclusion research in mixed conifer forests, herbivory (or lack thereof) may have influenced understory responses. In one of the few studies in our review both evaluating herbivory and finding short-term increases in plant cover, Mason et al. (2009) concluded that incidence of grazing was low, with no more than 15% of individual forbs and grasses displaying evidence of grazing. Two studies evaluating grazing in mixed conifer forests that had already been cut or burned reported major influences of grazing on plant abundance and composition. Kosco and Bartolome (1983) found that ungrazed Sierra Nevada clearcuts had 3 times the plant cover of clearcuts grazed by cattle and deer. Similarly, Riggs et al. (2000) found that understory biomass in cut and burned Oregon mixed conifer forest ungrazed for 27–30 years was double that of grazed areas. Species richness, on the other hand, often has been little affected or increased by grazing, usually through positive responses of annuals and other short-lived species (Riggs et al., 2000). More extensive research in *P. ponderosa* forests has supported these findings: when appreciable herbivores are present, plant abundance can be substantially reduced, individual species can decrease or increase in response to herbivory (Clary, 1975; Huffman et al., 2009), and plant richness often is less influenced or increases depending on the forest overstory (Bakker and Moore, 2007). Particularly in mixed conifer forest containing *P. tremuloides*, a tree whose recruitment is limited by browsing, herbivory could also influence post-treatment understory dynamics via effects mediated through tree structure (Coop et al., 2014). Where possible, overlaying herbivory treatments (including excluding large herbivores) with tree cutting and fire may augment insight into understory dynamics.

### 5.3. Pre-treatment vegetation and soil seed banks

Pre-treatment condition of the plant community is likely a major variable influencing post-treatment condition. Persistence and priority effects, or species present initially being difficult to displace, appear strong in western coniferous forests (Kreyling

et al., 2008; McGlone et al., 2012; Halpern and Lutz, 2013). This does not necessarily preclude new species from becoming established, but rather that species present initially persist through treatment even if their abundance is reduced (Dodson et al., 2007). Mechanisms including resprouting and tight links between soil seed banks and aboveground composition, promote species persistence (Lyon and Stickney, 1976; Fischer and Clayton, 1983; Bradley et al., 1992). The cutting + prescribed fire treatment in this review suggests species persistence, because plant abundance was usually reduced immediately after treatment, but species richness (driven by persistence with smaller components of new species) was typically maintained or increased (Fig. 3c and f).

Interestingly, in one of the few studies to directly correlate pre- and post-treatment vegetation within individual plots, Dodson et al. (2008) reported that difference between pre- and post-treatment understory cover and richness was negatively related to pre-treatment levels. In other words, plots with the least pre-treatment understory plant cover or richness generally increased the most after treatment (in some cases nearly equalizing out pre-existing differences), leading to the conclusion that treatments benefit the least vegetated areas the most (Dodson et al., 2008). This warrants assessment in other mixed conifer forests, because a different expectation could be that areas with the least pre-treatment vegetation respond the least, owing to sparse seed production, depleted soil seed banks, and low potential for vegetative propagation such as sprouting (Bossuyt and Hermy, 2001). Determining whether there is a critical amount of understory vegetation needed before treatment to produce a large response, or whether convergence occurs after treatment, may help explain variation in post-treatment dynamics. Moreover, better understanding which species are ‘persisters’ or ‘colonizers’ – likely a function of relative importance of aboveground vegetation and soil seed banks – may be useful for forecasting treatment influences given an initial assemblage of species (c.f. Dodson et al., 2007).

Studies that relate soil seed bank composition to aboveground vegetation, including before and after disturbance, can aid understanding plant community maintenance and recruitment mechanisms (Archibold, 1989; Stark et al., 2006; Abella et al., 2007). Further work is needed for detailed understanding of the role of seed banks in understory response to treatments (e.g., estimates of what proportion of the seed bank germinates following disturbance, or is lost to disturbance), and several studies have provided a baseline by quantifying soil seed bank composition in untreated mixed conifer forest. Overall conclusions from these studies suggest that soil seed banks in mixed conifer forests are usually not large (typically  $\leq 1000$  seeds  $m^{-2}$  for the upper 5 cm of mineral soil), but they can be species-rich (~30 to >80 species) and contain native perennials and shorter-lived species often associated with disturbance (Strickler and Edgerton, 1976; Kramer and Johnson, 1987; Stark et al., 2006; Abella and Springer, 2012). Compared to many other ecosystems, a unique feature of soil seed banks of mixed conifer forests is that they often contain appreciable amounts of native perennial species. For instance, native perennials constituted 75% (of 78) of taxa in soil seed banks of mixed conifer forests in Idaho (Kramer and Johnson, 1987) and 79% (of 39 taxa) in Nevada (Abella and Springer, 2012). Some of the dominant perennials, such as *Ceanothus velutinus* (snowbrush ceanothus) in Kramer and Johnson (1987), include species thought to be fire-stimulated (Conard and Radosovich, 1982; Weatherspoon, 1988). Some of the shorter-lived species dominant in mixed conifer seed banks, such as the annuals *Chamerion angustifolium* ssp. *angustifolium* (fireweed) and *Epilobium ciliatum* (fringed willowherb), are also stimulated by fire or disturbance to overstory or forest floor (Stark et al., 2006). These studies have further reported that >85% of taxa in soil seed banks were native (Kramer and Johnson,

1987; Stark et al., 2006; Abella and Springer, 2012). Collectively, findings suggest that: (i) the relatively small size of soil seed banks in mixed conifer forests may partly account for the typical lack of rapid increase in post-treatment vegetation; (ii) native species including perennials in the seed bank suggest longer term understory recruitment potential after treatments; and (iii) low amounts of non-native species in seed banks may relate to the observed low abundance of non-natives after treatments.

#### 5.4. Comparing cutting and prescribed fire, including disturbance-promoted species

Tree cutting and prescribed fire had similar overall influence on total understory cover and richness. If burns are sufficiently severe to reduce tree density, prescribed fire and cutting may not be that dissimilar in their influence on ecosystem properties affecting understory vegetation (Ma et al., 2010; Fulé et al., 2012; North et al., 2012). Both can expose mineral soil, via burning O horizons or during cutting operations (Cram et al., 2007; Laughlin and Fulé, 2008). Both also usually at least temporarily decrease total ecosystem nutrient pools (e.g., Clayton and Kennedy, 1985), but plant-available nutrients can increase (Gundale et al., 2006).

Species composition may represent the greatest potential for influences of cutting and prescribed fire to diverge, such as through germination cues. Some understory species of mixed conifer forests, including *Ceanothus integerrimus* (deerbrush) that is stimulated by heat (Kauffman and Martin, 1991) and *Penstemon* spp. stimulated by smoke (Abella et al., 2007), may be favored by fire. Six studies reported groups of native species abundant after prescribed fire or cutting + fire that are apparently fire-dependent, because the species were infrequent or absent in unburned forest, including after tree cutting alone (Lyon, 1966; Huisinga et al., 2005; Stark et al., 2006; Dodson et al., 2007; Knapp et al., 2007; Dodson and Peterson, 2010). These fire-stimulated groups were mainly forbs and included species such as: perennial forbs *C. angustifolium* (fireweed), *Claytonia perfoliata* (miner's lettuce), *Epilobium glaberrimum* (glaucus willowherb), *Pseudognaphalium canescens* (Wright's cudweed), and *Lotus crassifolius* (big deervetch); and the annual forbs *Epilobium brachycarpum* (tall annual willowherb), *Gayophytum diffusum* (spreading groundsmoke), and *Cryptantha simulans* (pinewoods cryptantha). It is possible that these species were once more common (at least ephemerally) in fire-prone historical forests.

Applying both cutting and prescribed fire resulted in the greatest invasion of non-native plants, but even in this treatment, non-native cover was low (Dodson and Fiedler, 2006; Collins et al., 2007; Dodson et al., 2008). Fiedler et al. (2013) hypothesized potential pathways of post-treatment non-native plant dynamics, including scenarios such as slight increases after treatment then declines through time, versus increases and persistence in the treated forest. Non-native dynamics may partly depend on identity of the invader, where perseverance of some species appears low (e.g., *Verbascum thapsus* [common mullein]), compared to high for species such as *Bromus tectorum* (cheatgrass, Fiedler et al., 2013). While non-natives are usually not prevalent in mixed conifer forests, non-native plants generally have increased in western North America (Keeley, 2006; Abella and Fornwalt, 2014). This increases chance that some will become established in mixed conifer forest, combined with expanding wildland-urban interfaces likely increasing opportunities for seed transport. Moreover, with reintroducing open stand structures and fire, sustainability of the current low invasion status of mixed conifer forests could be uncertain (Keeley, 2006). It should be noted, however, that untreated forest that burns in stand-replacing wildfire can become heavily invaded over time (McGlone and Egan, 2009). These observations suggest that: (1) monitoring non-native plant dynamics is warranted, (2)

consideration could be given to proactively treating incipient infestations of priority species as a precautionary approach, and (3) non-native abundance after severe wildfire is likely an appropriate benchmark against which to compare non-native abundance after tree cutting and prescribed fire treatments (Abella, 2014).

#### 5.5. Wildfire

Few studies of post-wildfire dynamics have been conducted in mixed conifer forests, and few of these met our inclusion criteria. The main unmet criterion was including either pre-fire data (difficult for unplanned events such as wildfires) or comparisons to unburned areas. Some studies not meeting inclusion criteria compared fire severities within a burned area, but this does not provide insight into actual effect of burning (relative to no burning), which was the focus of our analysis. We suggest that wherever possible, studies of wildfires include unburned areas for comparison that also can be monitored through time. On large wildfires exceeding tens of thousands of hectares, unburned areas may not exist nearby, yet measuring unburned areas as close as possible would represent unburned forest now extant on the landscape.

Some preliminary expectations for wildfire effects developed from extant research of wildfire influences on mixed conifer understories include reductions in shrub soil seed banks (Stark et al., 2006; Knapp et al., 2012), variable responses of shrub cover which might hinge on the pre-fire shrub community (Donato et al., 2009; Knapp et al., 2012; Crotteau et al., 2013; Walker et al., 2013), increased total species richness and forb abundance (Donato et al., 2009; Walker et al., 2013), and contingency of effects upon fire severity likely partly mediated through overstory tree mortality (Stark et al., 2006; Crotteau et al., 2013). Research also suggests probable increases in understory native plant cover and richness after severe burning where tree overstories are mostly or completely removed (Newland and DeLuca, 2000; Laughlin and Fulé, 2008; Fornwalt and Kaufmann, 2014). Stand-replacing fires, where in formerly frequent-fire forest containing old trees, are catastrophic from a forest ecosystem perspective, but may create species-rich understory communities for at least decades (Abella and Fornwalt, 2014).

#### 5.6. Is active revegetation warranted?

Short-term reductions in vegetation cover after treatment or reductions in certain species after wildfire may invoke consideration of seeding or planting nursery-grown plants to attempt actively accelerating plant establishment (Peppin et al., 2010). It should be noted that actively augmenting seeds or plants is only effective if plant propagules are actually limiting to plant establishment (Turnbull et al., 2000). If other factors, such as drought, overstory density, or herbivory are limiting, active revegetation is unlikely to have much influence. Seeding after wildfire in western forests has been controversial, partly from using non-native plants (or exotic genetics); it often is unclear if seeding is needed or interferes with natural recovery; and it can be expensive and prone to failure (Peppin et al., 2010). Using native seed can reduce some of this concern, but better understanding long-term understory dynamics (to evaluate if seeding is even necessary) and manipulating other factors such as slash or grazing to understand their effects on plant establishment after tree cutting or fire would be warranted. Another consideration, little discussed, is the possibility of identifying uncommon native species, such as those potentially associated with fire (or, conversely, vulnerable to severe fire in the case of wildfire), and focusing any active revegetation treatments on those species. Seeding has facilitated native plant establishment on discrete disturbances such as sterilized soil of burned slash piles (Korb et al., 2004; Fornwalt and Rhoades,

2011). Planting greenhouse-grown plants has effectively revegetated decommissioned forest roads, skid trails, landings, and post-tree thinning areas, where plant survival has exceeded 70% (Page and Bork, 2005; Abella and Springer, 2009). Using nursery-grown plants to create vegetated patches, which then can produce seed themselves, can be a more reliable revegetation strategy than attempting seeding across large areas. There may be a place for active revegetation in mixed conifer forest management, such as for areas severely disturbed by treatment operations, but possible disadvantages (including cost) need to be balanced against other strategies for promoting understories, including managing herbivory, treating slash, and controlling non-native plants.

### 5.7. Conclusion

Two of the most important factors in understory dynamics after tree cutting and fire in mixed conifer forests were time since treatment and specific operational aspects of treatments (e.g., whether cutting and fire were applied together, and amount of forest overstory removed). Understory measures often declined for the first few years after treatment, but subsequently increased if forest overstories had been reduced to well below 40–50% canopy cover. There are often fire-stimulated native species in the understory flora that are uncommon in long-unburned mixed conifer forests and after tree cutting alone, but that are stimulated by prescribed burns or wildfires. Non-native plants were generally sparse and subordinate in abundance to native species in both untreated forest and after cutting and prescribed fire, but long-term monitoring and precautionary non-native plant control warrant consideration if maintaining this status quo is a management goal. Based on our review of existing literature, further research needs include: (i) assessing effects of specific components of treatment operations (e.g., cutting intensity and residual spatial arrangements of trees, methods of slash treatment, grazing management) and their interaction on understory trajectories; (ii) comparing responses in moist versus dry mixed conifer forest; (iii) evaluating long-term similarities and differences between tree cutting and prescribed fire regimes and their combination; (iv) further identifying groups of native species benefiting from treatments or sensitive to treatment alternatives; (v) determining feasibility of forecasting treatment effects based on the initial plant community including seed bank composition; and (vi) more thoroughly understanding influences of wildfires. For operational monitoring of projects, early

monitoring is important to detect an initial surge in disturbance-promoted species (both native and non-native). However, the delayed increase in total understory plant cover and richness indicated that monitoring for at least 4 years after treatment is necessary to accurately appraise longer term trajectories of post-treatment understories. Monitoring both total understory measures and management-priority groups of species (e.g., fire-stimulated flora, or shrubs for browse) is useful for identifying whether further management (e.g., non-native species control) can provide competitive advantages to desired species groups. We conclude that native understory species, even if temporarily reduced in abundance, persist through tree cutting and prescribed fire and have benefited from these treatments after 5 years post-treatment, as long as forest overstories remain open.

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### Appendix A

Characteristics of 41 studies examining effects of tree cutting, prescribed fire, or wildfire in mixed conifer forests of western North America. Location, average precipitation, fire-return interval, tree species, relative proportion of understory growth form, and study design are provided. Studies are organized by general region from south to north, corresponding with Table 1 and map locations therein for Fig. 1.

Reference	Area <sup>b</sup>	Location <sup>c</sup>	PP (cm yr <sup>-1</sup> ) <sup>d</sup>	FI (yrs) <sup>e</sup>	Tree species <sup>f</sup>	Shrubs <sup>g</sup>	Herbs <sup>g</sup>	Units <sup>g</sup>	Design <sup>h</sup>
<i>Southwest</i>									
Cram et al. (2007)	NM	Sacramento Mtns	74	– <sup>i</sup>	AC, PM, PP	0	<1	cv %	0,1,0,0
Ffolliott and Gottfried (1989)	AZ	White Mtns	77	–	AC, AL, PCP, PE, PM, PP, PS	–	–	–	0,1,1,0,2
Huisinga et al. (2005)	AZ	Grand Canyon NP	65	5	AC, PE, PM, PP	–	–	–	0,1,0,0,2
Mason et al. (2009)	NM	Sacramento Mtns	70	–	AC, PM, PP, PS	5	6	cv %	0,1,1,0,1
Patton (1976)	AZ	White Mtns	76	–	AC, AL, PP, PS, PCP, PE, PM	–	11	g m <sup>-2</sup>	1,0,0,0,1
Thill et al. (1983)	AZ	White Mtns	69	–	AC, AL, PCP, PE, PM, PP, PS	–	–	–	0,1,1,0,3
<i>Sierra Nevada</i>									
Battles et al. (2001)	CA	Blodgett EF	158	–	AC, CD, PL, PM, PP	3	6	cv %	0,1,1,0,3

## Appendix A (continued)

Reference	Area <sup>b</sup>	Location <sup>c</sup>	PP (cm yr <sup>-1</sup> ) <sup>d</sup>	FI (yrs) <sup>e</sup>	Tree species <sup>f</sup>	Shrubs <sup>g</sup>	Herbs <sup>g</sup>	Units <sup>g</sup>	Design <sup>h</sup>
Bêche et al. (2005)	CA	Blodgett EF	156	7	CD, PL, PM, PP	–	–	–	1,1,0,0,0
Chiono et al. (2012)	CA	Sierra Nevada, Cascade Mtns	38–230	6–18	AC, CD, PJ, PL, PM, PP	–	–	–	0,1,1,0,2
Collins et al. (2007) <sup>a</sup>	CA	Blodgett EF	160	5	AC, CD, PL, PM, PP	9	6	cv %	1,1,1,0,1
Hurteau and North (2008)	CA	Yosemite NP, Teakettle EF	125	–	AC, AM, CD, PJ, PL	20	2	g m <sup>-2</sup>	1,1,1,0,0
Kauffman and Martin (1990)	CA	Blodgett EF, nearby sites	90–180	8–10	AC, PJ, PP, PM	–	–	–	1,1,1,0,1
Knapp et al. (2007)	CA	Sequoia NP	121	27	AC, AM, CD, PJ, PL, PP	3	14	cv %	1,1,1,0,1
Knapp et al. (2012)	CA	Shasta-Trinity, Lassen NFs	103	–	AC, AM, CD, PJ, PL, PM, PP	–	–	–	0,1,1,0,2
Knapp et al. (2013)	CA	Stanislaus- Tuolumne EF	103	< 9	AC, CD, PJ, PL, PP	–	–	–	1,0,1,0,3
Siegel and DeSante (2003)	CA	Sierra Pacific Industries	134	–	AC, CD, PL, PM, PP	–	–	–	0,1,1,0,2
Walker et al. (2012)	CA	Lake Tahoe Basin	81	–	AC, CD, AM, PJ, PL	–	–	–	1,1,0,0,2
Walker et al. (2013)	CA	Lake Tahoe Basin	87	–	AC, CD, PJ, PL	158	1	–	1,1,0,0,2
Wayman and North (2007)	CA	Teakettle EF	125	12– 17	AC, CD, PJ, PL	25	5	–	1,1,1,0,1
Webster and Halpern (2010)	CA	Sequoia/Kings Canyon NPs	105	2–30	AC, CD, PJ, PL, PP	3	9	cv %	1,1,1,0,3
Zhang et al. (2008)	CA	Blacks Mountain EF	46	–	AC, CD, PJ, PP	–	–	–	0,0,1,0,2
<i>California Cascades/Klamaths</i>									
Crotteau et al. (2013)	CA	Cascade Mtns	189	9–43	AC, CD, PL, PM, PP	–	–	–	0,1,1,1,3
Donato et al. (2009)	OR	Klamath-Siskiyou Mtns	150–300	5–75	AC, CD, PL, PM	15	5	–	0,1,0,1,1
<i>Northwest</i>									
Dodson et al. (2008) <sup>a</sup>	WA	Cascade Mtns	68	6–21	PM, PP	101	42	g m <sup>-2</sup>	1,1,1,0,1
Fonda and Binney (2011)	WA	Olympic NP	64	21	PM, TH	–	–	–	1,0,1,0,1
Hardman and McCune (2010)	OR	Blue Mtns	55	–	AG, LO, PM, PP	–	–	–	0,1,1,0,1
Harrod and Halpern (2009)	WA	Wenatchee Mtns	≫22	–	PM, PP	–	–	–	1,1,1,0,1
Metlen et al. (2004) <sup>a</sup>	OR	Blue Mtns	50	< 20	PM, PP	18	62	cv %	1,1,1,0,1
Scherer et al. (2000)	WA	Cascade Mtns	121	–	AG, AL, PM	–	–	–	0,1,1,0,1
Young et al. (1967), Hedrick et al. (1968)	OR	Blue Mtns	46	–	AG, PM, PP	1894	35	g m <sup>-2</sup>	0,1,0,0,1
<i>Central Rockies</i>									
Ayers et al. (1999), Bedunah et al. (1999)	MT	Lick Creek Demo Area	53	1–30	PM, PP	–	–	–	1,1,0,0,0
Metlen and Fiedler (2006) <sup>a</sup>	MT	Lubrecht EF	50	–	LO, PC, PM, PP	10	10	–	1,1,1,0,1
Gordon (1976)	MT	Absaroka Range	>40	–	PE, PM	–	–	–	1,0,0,0,1
Lyon (1966)	ID	Sawtooth NF	43	–	PM	–	–	–	1,1,0,0,1
Newland and DeLuca (2000)	MT	Lick Creek, Lolo NF	62	13– 50	PM, PP	–	–	–	0,1,1,0,2
Steele and Beaufait (1969)	MT	Lubrecht EF	50	–	LO, PM	–	–	–	0,1,1,0,0
<i>Interior British Columbia</i>									
Ducherer et al. (2009)	BC	Near City of Kamloops	30	10– 12	PM, PP	1	33	g m <sup>-2</sup>	1,1,1,0,1
Ducherer et al. (2013)	BC	Near City of Kamloops	30	–	PM, PP	0	101	g m <sup>-2</sup>	1,1,1,0,2
Lochhead and Comeau (2012)	BC	St Mary River Research Trial	38	–	LO, PC, PE, PG, PM, PP	7	21	–	0,1,1,0,3
Page et al. (2005)	BC	East Kootenay region	38	5–50	PM, PP	15	20	cv %	1,0,0,0,0

(continued on next page)

## Appendix A (continued)

Reference	Area <sup>b</sup>	Location <sup>c</sup>	PP (cm yr <sup>-1</sup> ) <sup>d</sup>	FI (yrs) <sup>e</sup>	Tree species <sup>f</sup>	Shrubs <sup>g</sup>	Herbs <sup>g</sup>	Units <sup>g</sup>	Design <sup>h</sup>
Stark et al. (2006, 2008)	BC	Near City of Kamloops	30–85	–	PC, PM, PP	–	–	–	0,1,1,1,0

<sup>a</sup> Fire and Fire Surrogate study sites: Blodgett, Collins et al. (2007); Mission Creek, Dodson et al. (2008), Dodson and Peterson (2010), Agee and Lolley (2006); Blue Mountains, Metlen et al. (2004), Youngblood et al. (2006); Lubrecht, Metlen and Fiedler (2006), Dodson and Fiedler (2006), Dodson et al. (2007), Gundale et al. (2006).

<sup>b</sup> U.S. states and Canadian province: AZ, Arizona; NM, New Mexico; CA, California; OR, Oregon; WA, Washington; MT, Montana; ID, Idaho; BC, British Columbia.

<sup>c</sup> EF, experimental forest; NF, national forest; NP, national park.

<sup>d</sup> Long-term average precipitation provided by papers, or if in italics, our estimated average precipitation based on PRISM using study location provided in papers (e.g., geographic coordinates, distance from nearest city).

<sup>e</sup> Mean or range of mean fire-return interval provided in papers.

<sup>f</sup> AC, *Abies concolor*; AG, *Abies grandis*; AL, *Abies lasiocarpa*; AM, *Abies magnifica*; CD, *Calocedrus decurrens*; LO, *Larix occidentalis*; PC, *Pinus contorta*; PE, *Picea engelmannii*; PG, *Picea glauca*; PJ, *Pinus jeffreyi*; PL, *Pinus lambertiana*; PM, *Pseudotsuga menziesii*; PCP, *Picea pungens*; PP, *Pinus ponderosa*; PS, *Pinus strobiformis*; TH, *Tsuga heterophylla*.

<sup>g</sup> Amount of understory vegetation before treatment or in controls (or pre-treatment in controls), shown as percent cover (cv %) or biomass (g m<sup>-2</sup>). Forbs and graminoids were combined in many studies and are shown here as herbaceous vegetation.

<sup>h</sup> Study design as: 1 for yes for pre-treatment data collected, controls present, replication of treatments across independent sites, replication across some environmental gradient (e.g., soil parent material, or fire severity class for wildfire), and, for duration, <2 years = 0, 2–3 years = 1, 4–9 years = 2, and ≥ 10 years = 3. Duration is the longest time since treatment that the last post-treatment measurement was made.

<sup>i</sup> – signifies not provided in a study.

## Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.09.009>.

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