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The effects of forest restoration on ecosystem carbon in western North America: a systematic review

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Highlights:

1. Restoration treatments decrease forest C pools, with limited evidence of recovery
2. Long-term carbon loss may be reduced when post-treatment wildfire is present
3. Few empirical studies exist at large spatial scales or over time periods >25 years
4. The response of deeper mineral soil to treatments remains a major knowledge gap
5. Need consistent methodology for measuring and reporting C pools

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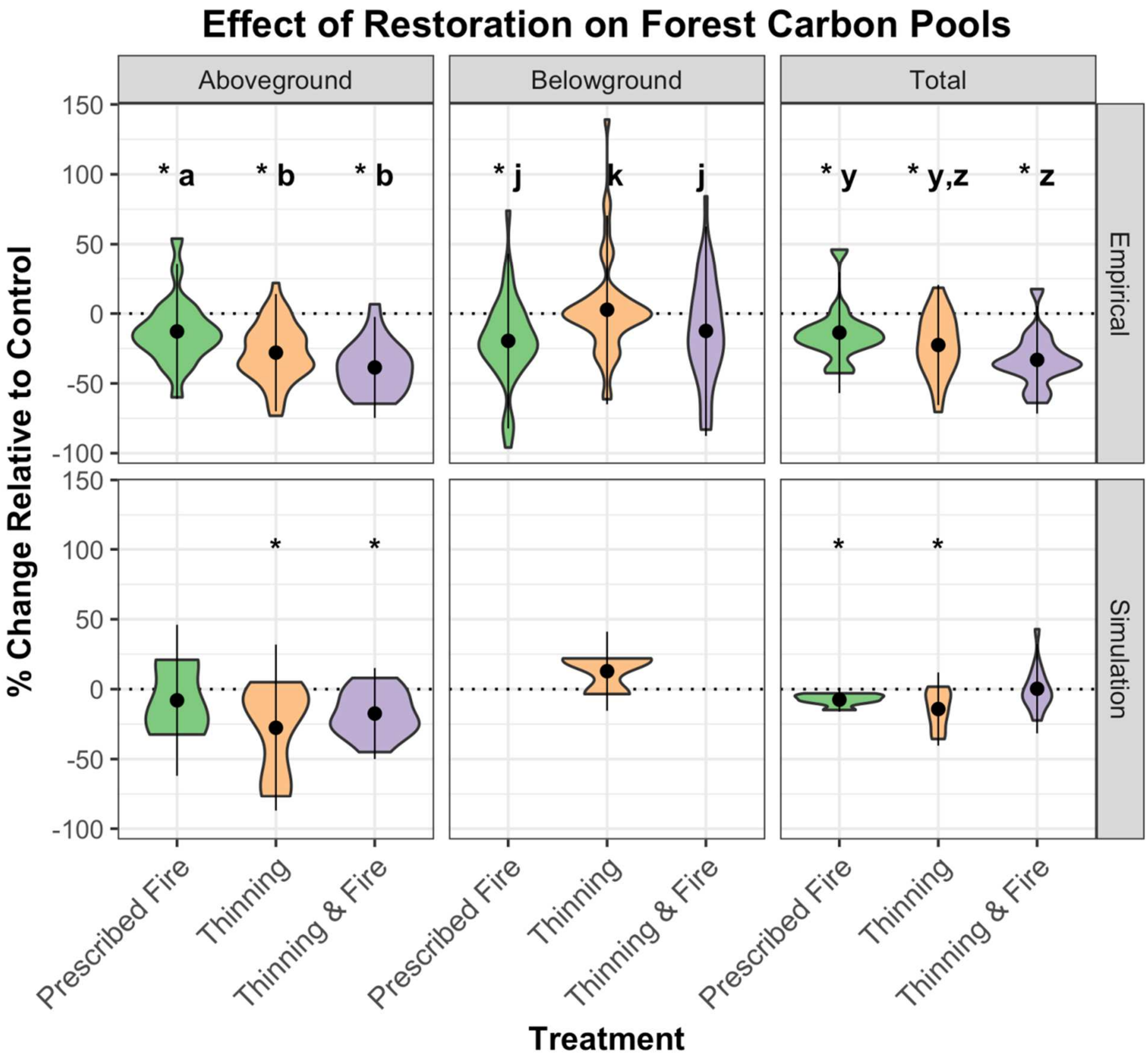
ABSTRACT

Ecological restoration has become an overarching management paradigm for sustaining the health and resilience of forests across western North America. Restoration often involves mechanical thinning to promote development of complex habitats in moist, productive forests and mechanical thinning with prescribed fire to reduce fuels and restore natural disturbance regimes in dry, fire prone forests. This systematic review quantified the impact of restoration treatments on forest ecosystem carbon (C) stocks and identified factors that moderate treatment effects across spatial and temporal scales. Our review process identified 73 studies to be included for analysis, from which we calculated 482 estimates of treatment effect size. We found that restoration treatments significantly reduce C. Prescribed fire had larger impacts on belowground than aboveground carbon pools, while thinning and combined treatments had larger impacts on aboveground pools. The available literature is highly skewed toward shorter timescales (<25 years after treatment), small spatial scales, and is geographically concentrated: 41% of estimated effect sizes came from studies in the Sierra Nevada. Thinning had similar effects on forest carbon in dry forests and moist forests. The relative magnitude of total C losses was significantly less from simulation than empirical studies, although simulations also mostly evaluated long-term impacts (>75 years after treatment) while empirical studies mostly looked at short term (<25 year) effects. Post-treatment wildfire significantly reduced the percentage of carbon lost relative to controls in the aboveground pool. Long-term, treated stands only recovered to control levels of carbon when wildfire was present. Returns on the carbon debt imposed by thinning and prescribed fire depend on the nuances of the treatments themselves but may also depend upon treatment intensity and the frequency and intensity of future wildfire. Ecological restoration in forests across the western US has to carefully balance the budget of ecosystem carbon with competing objectives such as improved wildlife habitat, reduced risk of severe wildfire, and other ecosystem services.

GRAPHICAL ABSTRACT



1. Introduction

1.1. Forests and carbon sequestration

Managing public forestlands to enhance carbon sequestration has been proposed as a method to reduce atmospheric CO_2 concentrations and mitigate threats from climate change (Brown, 1996; Griscom et al., 2017; Vitousek, 1991). Forest ecosystems play an important role in carbon sequestration and storage, exerting strong control on the evolution of atmospheric CO_2 and serving as large terrestrial carbon sinks (Pan et al., 2011). Forests can act as carbon sinks by accumulating carbon in living or nonliving organic matter and in soils (Pacala et al., 2001). In addition, carbon outputs from forests may be stored in ways that delay or prevent carbon from returning to the atmosphere, such as wood products and eroded surface sediments deposited in reservoirs, rivers, and floodplains (Cole et al., 2007; Hurtt et al., 2002; Pacala et al., 2001). At large spatial and temporal scales, natural ecosystem dynamics and disturbance regimes may tend to keep forest carbon in relative balance. But recently, forest lands within the United States are estimated to be a net sink for carbon due to a variety of factors including forest growth, land use changes such as reforestation of abandoned farmlands, and the accumulation and encroachment of woody vegetation caused by fire suppression (Hurtt et al., 2002; Pacala et al., 2001; Pan et al., 2011).

1.2. Moist and dry forest disturbance regimes & degradation

Forests are often managed based on their disturbance regimes and ecosystem characteristics. In the Western US, there is a major divide in ecosystem productivity and management between moist and dry forests. Moist forest ecosystems (MFs) typically occur in the Coast Range, western Cascades, and northern Rocky Mountains and have a historical disturbance regime characterized by large, infrequent wildfires which include extensive, severely burned areas that result in stand-replacement conditions (Agee, 1996). Following the historic fire regime classification of Barrett et al. (2010), these forests are often classified as Fire Regime Group V (FRG V; 200+ year frequency and high severity) or Fire Regime Group IV (FRG IV; 35-100+ year frequency and high severity). These forests developed structurally complex features over the course of centuries (Franklin et al., 1981; Waring and Franklin, 1979). Beginning in the mid-1800s, many MFs experienced intensive logging or were lost to development (Strittholt et al., 2006). Currently, many landscapes with MF are dominated by young plantations low in structural and biological diversity, and deficient in both early-seral and late-successional habitat compared to a historic range of variation (HRV) (Bormann et al., 2015; DeMeo et al., 2018; Franklin and Johnson, 2012).

Dry forest ecosystems (DFs) are typically found east of the Cascade Range in western North America and historically experienced low-and mixed-severity fires at frequent intervals (Agee, 1996; Perry et al., 2011). The historic fire regimes are classified as either Fire Regime Group I (FRG I; 0-35 year frequency and low severity) or Fire Regime Group III (FRG III; 35-100+ year frequency and mixed severity) (Barrett et al., 2010). Fire suppression and other factors including intensive grazing and harvesting over the last 150 years have shifted forest composition toward more late seral species (such as white and red firs), allowed trees to become denser, and promoted uncharacteristically large and severe wildfires due to fuel accumulation (Miller et al., 2009; Stephens, 1998). The number of fires and total fire area per year have increased over the past several decades (Dennison et al., 2014).

Western North America is home to many species of large, long-lived conifers (Waring and Franklin, 1979). For the most part, the precipitation gradient across the Cascade Range separates the more productive MFs from the more arid and continental interior west where DFs dominate. However, both forest types exist in a continuum of possible compositions, structures, and functions, and likewise contain a mix of disturbance types, frequencies, and intensities (Waring and Franklin, 1979). Although MFs and DFs differ in many ways, both have become increasingly susceptible to threats other than wildfire. Forests across western North America are experiencing increasing tree mortality rates due to factors such as drought stress and insects (Van Mantgem et al., 2009). Large trees in particular are being threatened by disturbance, presenting a concern to forest managers due to their large carbon stores (Smithwick et al., 2002; Stephenson et al., 2014) as well as the long time needed for development of unique structural features (Franklin and Johnson, 2012).

1.3. Managing for ecological resilience

Promoting ecological resilience has become a central management objective on public forestlands in the United States in light of the combined effects of past disturbances and projected effects of climate change (DeMeo et al., 2018; Franklin and Johnson, 2012; Hessburg et al., 2015). Broadly, resilience is interpreted as a measure of the capacity of an ecosystem to regain its pre-disturbance composition, structure, and ecological functions (Holling, 1973). Restoration of degraded habitat and ecosystem function is necessary in many large forested landscapes across western North America (Churchill et al., 2013; DeMeo et al., 2018; Franklin and Johnson, 2012; Haugo et al., 2015). Forest restoration strategies differ broadly between MFs and DFs due to their different characteristic disturbance regimes (Franklin and Johnson, 2012). The driving ecological restoration strategy for MFs includes reserving older forests and thinning young forests to accelerate the development of structural complexity (Churchill et al., 2013; DeMeo et al., 2018; Franklin and Johnson, 2012). In DFs, the main restoration strategy calls for treatments that promote older trees, reduce stand densities, shift composition towards fire-and drought-tolerant tree species, and incorporate spatial heterogeneity (Franklin and Johnson, 2012; Haugo et al., 2015). However, although the strategies differ among ecosystems, the actual restoration treatments are broadly similar: reducing the density of present day forest stands using mechanical thinning, prescribed fire, or a combination of the two to alter forest structure and composition and restore or accelerate natural ecological processes. While prescribed fire (alone or in combination with mechanical thinning) is a necessary component of restoring DF (Hessburg et al., 2015), it is rarely used within MFs.

1.4. Impacts of management on carbon

Carbon storage in long-term forest pools is determined by the balance between carbon accumulated through photosynthesis, carbon loss through decay, and offsite removal or non-biological carbon emissions, including pyrogenic emissions (Carlson et al., 2012). Fire removes fuel from a stand in the form of emissions and converts portions of biomass from standing live trees to standing dead trees due to fire-caused mortality. Over time, dead trees fall to the forest floor and accumulate as fuels. Additionally, when forests burn, some of the stored carbon is emitted to the atmosphere (Wiedinmyer and Neff, 2007) and later through the decomposition of fire-killed biomass (Harmon and Marks, 2002). Disturbances can also affect future carbon cycling processes. For example, wildfire impacts the growth of residual trees by volatilizing some soil nutrients, increasing available light, increasing available growing space (Reinhardt and Holsinger, 2010), and altering hydrological processes like infiltration (Robichaud, 2003) and erosion (Berhe et al., 2018).

Restoration treatments are conducted for a range of ecological objectives. Tree harvest removes some material from a site and typically converts some biomass from standing live to dead surface material, although some methods remove most of the harvested material from a site (Reinhardt and Holsinger, 2010). Since they remove or consume biomass, they incur a debt of ecosystem carbon compared to their pre-treatment condition (Reinhardt and Holsinger, 2010; Wiechmann et al., 2015). Whether the ecological objectives outweigh the carbon debt of restoration treatments is unclear. However, managing forests for climate change mitigation and protecting carbon stocks from long-term loss due to pathogens, drought, and wildfire requires assessing potential short- and long-term trade-offs of treatments on carbon pools, fire risk, and ecosystem services such as biodiversity and water (Reinhardt and Holsinger, 2010). Furthermore, the amount of carbon removed by treatments and the time needed for forests to re-sequester that carbon affect the long-term carbon costs and benefits of restoration treatments (Hurteau and North, 2010). It is important to recognize the difficulty of predicting ecosystem dynamics resulting from disturbances such as wildfires or droughts that can induce large, rapid losses of terrestrial carbon and ecosystem function (Breshears and Allen, 2002; Millar and Stephenson, 2015). Some of the uncertainties in projecting forest carbon dynamics into the future – and thus the recovery of carbon removed due to treatments – include the effects of current and past land-use change, fire regimes, and forest management practices on the rates of carbon flux (Foster et al., 2003).

1.5. Objectives

We conducted a systematic review (*sensu* Pullin and Stewart, 2006) to quantify the effects of forest restoration treatments on storage of forest carbon (hereafter C). This involved assessing the impacts of thinning, prescribed fire, or combined treatments (thinning & fire) on the aboveground, belowground, and total ecosystem C stocks in forests of western North America. Aboveground C was calculated as the sum of live tree stems, snags, course and fine woody debris, and understory C sub-pools; belowground C was the sum of O horizon, mineral soil, and root C sub-pools; total C was the sum of all sub-pools. Our research questions were:

1) To what degree will ecological restoration treatments change forest ecosystem C stocks across temporal and spatial scales?
2) Do moist forest and dry forest ecosystem C stocks differ in their response to ecological restoration treatments?
3) What ecological and forest characteristics (fire regime, seral stage, fire resistance, and drought and shade tolerance) moderate the effect of ecological restoration treatments on forest ecosystem C stocks?
4) How long do forest C pools take to recover from restoration disturbances, both with and without wildfire?

2. Methods

2.1. Systematic Review Framework

We used a systematic review, following the framework developed by Pullin and Stewart (2006), to generate an unbiased assessment of the effects of forest restoration treatments on C stocks. A review protocol (Supplementary Material) was prepared with stakeholder input from The Nature Conservancy and the U.S. Forest Service Pacific Northwest Region during preliminary planning meetings. The protocol outlined the process for planning, conducting, and reporting results from the review. Our initial search criteria were based on forest type, intervention, geographic location, and C metrics. For each criterion, we developed a set of relevant keywords (Table 1) for the database queries described in section 2.2.

2.1.1. Geographic & Ecosystem Scope

Geographic scope was limited to forested ecosystems in western North America. Ecosystem scope was limited to temperate conifer forests based upon physiognomic characteristics, climatic and disturbance regimes, and species composition (Table 1). Forests in historic Fire Regime Groups IV and V were considered roughly analogous to moist forests while those in historic Fire Regime Groups I and III were analogous to dry forests (Barrett et al., 2010).

2.1.2. Management Interventions

The interventions of interest were restoration-focused management activities that mimic natural ecological disturbance regimes to restore and maintain forest structure and composition within historical range of variation (HRV) reference conditions specific to studied forests. Specifically, we focused on mechanical thinning and prescribed fire, separately and in combination (Table 1). Interventions could be applied to a field site or simulated across a landscape. For simulation studies, we collected and evaluated the longest time-step reported, as we were particularly interested in the medium-to-long-term response of forest C to treatment. We did not specify a maximum thinning intensity as long as some trees were retained (i.e., clearcuts were excluded). We did not include laboratory simulations of fire.

2.1.3. Counterfactuals

We identified consistent counterfactuals against which to evaluate the interventions. Usually, the counterfactuals consisted of no active management with full fire suppression and were expressed either by measurement of a control area at the same time as the treated area or by a pre-treatment measurement of the treated area. However, for simulations at landscape and ecoregion scales, the heterogeneity in historic land uses made comparison to the previous counterfactual impossible; these studies instead compare management scenarios to "business-as-usual" when calculating effect sizes. Business-as-usual refers to indefinite continuation of present management regimes over large spatial scales, including clearcutting on many private timberlands, little-to-no cutting on federal forest lands, and prolonged wildfire suppression. In addition, where wildfires occurred post-treatment and impacted both the treated and control areas, we considered an additional counterfactual: no active management followed by wildfire. The counterfactuals were not included in our initial searches but were a criterion during article screening.

2.2. Database Queries

We systematically searched the CAB Abstracts and Web of Science databases for original research published through December 2017 that investigated the effects of mechanical thinning and prescribed fire on C stocks. We selected empirical and simulation studies published within peer-reviewed scientific journals. In keeping with the review framework, published literature reviews and government gray literature (e.g., US Forest Service General Technical Reports) were not included.

To maximize our search returns, we combined all search terms through Boolean operations (Table 1). Duplicate articles were eliminated. Article titles and abstracts were screened to remove articles that met our inclusion criteria incidentally without providing relevant data for this review (e.g., a paper that mentions *Pinus ponderosa* but focuses on forests outside North America). We excluded articles that (1) were from ecosystems or locations not located in western North America or did not include conifer species, (2) did not include an applicable management treatment, (3) did not report on C stocks (e.g., only reported C fluxes), (4) were review articles, or (5) did not include an appropriate counterfactual (e.g., no pretreatment or control measurement). Articles that remained after this initial screening received a more detailed review of the article text to determine whether they should be retained or excluded.

For each article that met our inclusion criteria, we extracted and entered information in a formal rubric. We began by determining which carbon pool(s) the article reported on – details in section 2.3. We then recorded information about the management intervention, counterfactual, spatial scale of study, time since intervention, historic fire regime, presence or absence of wildfire, forest type, and forest ecosystem characteristics (major conifer species present and associated seral status, fire resistance, shade tolerance and drought tolerance of the assemblage) (Table 2). Forest attributes such as seral status and fire resistance were determined for each dominant/co-dominant species in the forest canopy based upon the ecological classification of Minore (1979) and the USFS Fire Effects Information System (https://www.feis-crs.org/feis/). Forests with multiple species were defined as intermediate if the tree species mixture include several in different classes.

2.3. Percentage Change, Carbon Pools, and Sub-pools

We quantified the effect of treatments on aboveground, belowground, and/or total C pools by computing the percentage difference between a given treatment and its counter-factual. Hereafter, we refer to this metric as “effect size”. We tallied the specific C sub-pools measured in each paper but computed effect sizes using the broader categories of aboveground C, belowground C, and total C. Aboveground C included live tree C, dead tree C, understory C (e.g., shrubs, herbs), and/or woody debris C. In several instances, root C was also included in the aboveground pool (e.g., when live tree C that included both aboveground and belowground components was reported in one aggregated number). Belowground C included mineral soil, the O horizon (e.g., duff or litter), and roots if reported separately. When estimates were reported for one or more sub-pools in both the aboveground and belowground C pools, we summed them to provide a measure of total C. In several cases, studies reported *only* a combined metric of C which included some (or all) aboveground and belowground components; we recorded this as total C (Figure 3).

Effect sizes were calculated using mean values for treatments and counterfactuals. While effect sizes in a meta-analysis often account for sample size and variation, the effect size presented is unweighted because many studies we included in our review did not report those details. Where possible, data were obtained directly from the article text, tables, or supplementary material. If data were only reported in a figure, we extracted values using WebPlotDigitizer (Rohatgi, 2017). Effect sizes were calculated for the longest time step available for simulation studies. Effect sizes for treatments compared to control (either with or without wildfire present) were calculated using Equation 1, where *Treatment* and *Control* are the values for the relevant C pool in the treated area and the untreated control.

$$\frac{Treatment - Control}{Control} \times 100 \qquad (1)$$

Effect sizes for treatments compared to pretreatment were calculated using Equation 2, where *Treatment (Pre)* and *Treatment (Post)* are the values for the C pool of the same area before and after the intervention.

$$\frac{Treatment\ (post) - Treatment\ (pre)}{Treatment\ (pre)} \times 100 \qquad (2)$$

For a single paper, multiple comparisons were recorded based upon the number of different treatments, presence of pretreatment data, number of separate sites, and the number of C pools reported. For example, a paper evaluating the effect of a thinning treatment on all three pools at one site could be recorded as up to six effect sizes in the rubric – three relative to the untreated control and three relative to the pretreatment values in the treated area.

2.4. Statistical Analysis

The effect of treatments on forest C pools was evaluated using ANOVA to compare among treatments and two-sided *t*-tests to determine whether effect sizes differed from zero. This analysis was performed separately for empirical and simulation study results. Data were evaluated for normality using the Shapiro-Wilk test, and a cube root transformation was applied to non-normal variables prior to analysis. We used this transformation because it can be used with negative values; only three tests for difference from zero required transformation. Significant ANOVA tests were followed by post-hoc multiple comparisons using Tukey's HSD.

To examine which moderating variables (Table 2) significantly alter the response of each forest C pool to treatment, we used a back-fitting model selection procedure with a linear mixed model. We designated paper ID as a random effect to account for among-study differences such as which sub-pools were included and how many effect sizes were calculated; this term was retained throughout model selection. All other terms were designated as fixed effects. Model selection was completed in two stages because there was not enough power to simultaneously evaluate all potential variables of interest. In the first stage, factors other than stand attributes were evaluated and eliminated in stepwise fashion. The data were too unbalanced to test most interactions among factors, but interactions between study type and other factors were included. The final model from the first stage served as the base model for the second stage, testing the effects of stand attributes, again evaluated and eliminated in a stepwise fashion. We considered tests significant at α=0.05. All statistical analyses were performed in R (R Development Core Team, 2017). Mixed effects models were constructed using the lmerTest package (Kuznetsova et al., 2017) with back-fitting via the step function, and denominator degrees of freedom were estimated with the Satterthwaite method. Estimated marginal means analysis with the ls_means function was used to complete post-hoc tests on significant factors.

3. Results

3.1. Search Results

Almost 3200 articles were returned by our search criteria (Figure 1). After deleting 225 duplicate citations, we applied our inclusion/exclusion criteria to the titles and abstracts of the articles and eliminated 2598 articles. Detailed reviews of the full text of the remaining papers led to the removal of another 286 articles. The final set included 73 papers that met our criteria. These papers were published between 1987 and 2017 in 22 journals, the most common of which was *Forest Ecology & Management* (22 papers). The number of effect sizes ranged from 1 to 124 per paper (median = 3, mean = 6.6), for a total of 482.

More articles reported measures of belowground than aboveground C (42/73 vs 33/73). Only 41% of articles (30/73) reported total C. There were substantial differences among articles in terms of which C sub-pools were included in each pool (Figure 2). The aboveground pool was almost always based upon live tree carbon (31/33 articles), usually included snags (20/33) and woody debris (23/33), but only rarely included understory C (10/33). Roots were sometimes included (8/33), mostly in studies using allometric equations to calculate tree biomass. The belowground pool generally included both the O horizon (litter & duff layer) (30/42) and mineral soil (31/42), although studies were more likely to measure one rather than both of these sub-pools. The average depth of soil sampling was 15 cm. Roots were rarely included in this pool (6/42) because they were not usually reported separately from live tree carbon. For the total pool, the least commonly represented sub-pools were mineral soil (16/30), understory (17/30), and roots (18/30). Only four studies included all sub-pools. For all subsequent results and discussion, we refer to 'Aboveground C,' 'Belowground C,' and 'Total C' to represent the subset of studies grouped in Figure 2, with the caveat that these groupings do not necessarily capture all components of these pools in every study.

3.2. Influence of Counterfactual on Effect Size

The magnitude of some effect sizes differed significantly depending on whether the treatment was compared to its pretreatment value or to a control (Supp. Figure 1). Treatments lost more aboveground and total C relative to control than relative to pre-treatment values, but there was no difference in loss of belowground C relative to pretreatment values or controls. Given this difference between counterfactuals, all subsequent statistical tests focused on effect sizes calculated relative to control. The control was also the most common counterfactual in our dataset: 355 of the 482 effect sizes were calculated relative to control.

3.3. Response of Forest C Pools to Restoration Interventions

Restoration treatments had different effects on forest C pools. In summarizing the overall patterns here, we report the results from empirical and simulation studies separately.

On average, empirical studies occurred within 10 years of treatment. In these studies, prescribed fire significantly decreased C in all C pools (Table 3: tests of difference from zero). Thinning had a mixed effect: the aboveground and total pools significantly decreased in response to treatment but the belowground pool was not affected. Thinning & Fire resulted in significant losses of C in the aboveground and total pools, but the opposing effects of fire and thinning treatments resulted in no statistically significant loss of belowground C for the combined treatment. Comparisons among treatments indicated that prescribed fire generally had a different effect than Thinning or Thinning & Fire (Table 3: comparisons among treatments). Prescribed fire did not reduce the aboveground C pool as much as the other treatments but had greater effects on belowground C. Losses of total C were significantly greater for the combined treatment than for prescribed fire alone.

Simulation studies generally examined longer time frames (112 years on average), were less common, and focused almost exclusively on the aboveground and total C pools; only 4 effect sizes explicitly reported changes in belowground C. Even over the timeframes examined in simulations, there were significant reductions in aboveground C due to the Thinning and Thinning & Fire treatments and a reduction in total C in response to Thinning (Table 3: tests of difference from zero). Treatments did not differ in terms of effect on C pools.

Model selection results are presented separately for each C pool in Table 4, and are reported here for each moderating variable.

3.4. Influence of Post-Treatment Wildfire on the Magnitude of Treatment Effects

The presence or absence of post-treatment wildfire was a significant moderator of changes in the aboveground C pool but not of the belowground or total C pools (Table 4). Furthermore, the effect of wildfire on aboveground C varied with study type: the losses of C due to treatment were reduced in the presence of wildfire in simulations, which typically cover larger spatial scales and longer timeframes but not in empirical studies (Figure 3).

3.5. Distribution of Observations by Spatial and Temporal Scale

Most of the studies returned by this systematic review were conducted at small (<100 ha) spatial scales, and thus there is a bias towards the stand scale in the results. This is largely because most empirical studies were performed in individual forest stands. The vast majority of studies conducted at larger scales were simulation studies. Spatial scale had a significant impact on the response of aboveground C to treatments (Supp. Figure 2). Empirical data at larger spatial scales often include confounding factors (such as the presence of wildfire, or differences in land ownership and forest conditions) that are difficult to control for, not to mention the inherent spatial heterogeneity in these forest systems. Furthermore, studies were not evenly distributed across ecoregions in western North America (Figure 4). Many of the studies (41%) were from the Sierra Nevada ecoregion.

Articles examined the effects of restoration treatments from < 1 year after treatment to 1500 years later. There were not significant trends in response to treatment over time for any C pool, although there was a significant interaction between Time and Study Type (Table 4; Supp. Figure 3). Most empirical studies (95%) ran for 25 years or less, whereas most simulation studies (89%) ran for more than 75 years. There is a gap in data over time between 25 and 75 years after treatment for all treatments, largely reflecting the long timeframes examined by models and the lack of multi-decadal empirical studies (Figure 5).

3.6. Forest Attributes Impact C Response to Restoration

Several forest attributes had significant impacts on the response of aboveground and belowground C, but not total C, to treatment.

Aboveground C was affected by seral stage, though this also varied between study types (Table 4). Early seral forests lost more C in response to treatment than mid/late seral forests (Figure 6). Seral status had a larger impact in simulation rather than empirical studies, perhaps because few simulation studies remained dominated by early seral species at the end of the simulation.

Fire resistance classes had differential effects on aboveground and belowground C (Table 4). For aboveground C, high fire resistance forests (those dominated by Douglas-fir, Jeffrey pine, ponderosa pine, and western larch) lost more C in response to treatment than medium resistance forests (Supp. Figure 3). However, for belowground C, medium fire-resistant forests lost more C than high resistance forests. Forests with low fire resistance tended to have large losses of C, but the number of effect sizes was insufficient to differentiate them from other fire resistance classes.

Shade tolerance status was a significant factor controlling the belowground C response to treatment (Table 4). Forests dominated by low shade-tolerant species saw greater losses of carbon compared to medium shade tolerant (mixed conifer) forests (Supp. Figure 4). There were not sufficient studies examining high shade tolerant forest to differentiate these from other shade tolerance classes.

3.7. Effect of Forest Type and Fire Regime

Thinning studies were conducted in both moist and dry forests, but effects did not differ between them for any of the C pools (Table 4; Supp. Figure 5).

Fire regime group was not related to effect size for any of the C pools (Table 4). However, sufficient studies have not been conducted in all fire regimes: only 4 observations were available for aboveground C in FRG III and only one in FRG IV. Further study in fire regime group III and IV is needed before any definitive conclusions can be drawn.

4. Discussion

4.1. Response to Treatments

Our results show that restoration treatments affect ecosystem carbon stocks differently. Aboveground C was reduced by all treatments but particularly by thinning or thinning & fire.

Prescribed fire was the only treatment to reduce belowground C, yet reduced total C by the least among all three treatments. The effect of prescribed fire on belowground C reflects the direct consumption of surface soil C, especially in forests that are high in fuels. Prescribed fires have to be completed under moderate weather conditions that permit low- to mixed-severity fire effects to achieve ecological objectives without causing undue mortality in overstory trees, although individual prescriptions vary depending on the objectives of the burn (Martin and Dell, 1978; Walstad and Radosevich, 1990). Generally, conditions are chosen to promote burning when fire behavior is expected to be low so that the fire remains in the understory and mostly consumes surface fuels.

Thinning alone reduced aboveground and total carbon but had no effect on belowground carbon. The increased response of aboveground and total carbon to thinning represents the direct removal of live tree biomass, which was the most commonly included sub-pool for both pools (Figure 2). Restoration strategies should consider the impacts of treatments on the proportion of carbon remaining in each sub-pool as well as the spatial heterogeneity after treatment. The ability of thinning to achieve targeted reductions in specific sub-pools, such as understory trees, may provide a benefit to forest managers using this method. However, unless thinned material is removed from the site it is transferred to other sub-pools, notably the woody debris and forest floor. In surface mineral soil, there can be significant but small losses of C following thinning, although this response is soil-type specific (James and Harrison, 2016). Little is known about treatment effects on the substantial pool of carbon in deeper soil (>30 cm).

The thinning & fire treatment had similar effects as thinning, suggesting that the effects of thinning exceed those of prescribed fire for aboveground C. This combination treatment is commonly used to reduce wildfire hazard in dry forests that are too dense for prescribed fire alone. Our findings suggest that forest restoration treatments may reduce some forest carbon pools over certain periods of time, particularly at the stand-level. The error estimates of the effect sizes are quite large as there is variation among studies in terms of which sub-pools were measured, as well as differences in the time since treatment and presence/absence of post-treatment wildfire. A more detailed analysis of the effects on individual sub-pools would be a valuable extension to this work, as the relative size and stability of C varies among sub-pools (e.g., live vs. dead trees).

Although restoration treatments remove C, there is a tradeoff between the carbon lost during treatments and the ability to protect carbon stocks in light of potential future disturbances (Mitchell et al., 2009). For example, successful fuel reduction treatments will retain a higher proportion of carbon as live vegetation following wildfire, prolonging the realization of potential carbon benefit of fuel treatments (Carlson et al., 2012). More work is needed to address this issue, particularly in moist forests that are becoming increasingly fire prone.

4.2. Thinning in Moist and Dry Forests

Our systematic review found that moist forests (MFs) and dry forests (DFs) responded similarly to thinning with respect to carbon pools. It is important to consider the results in light of future forest development on these landscapes and the other ecological objectives thinning treatments are meant to address. In MFs, restoration treatments have the potential to enhance structural complexity and promote many ecological characteristics beneficial to wildlife (Franklin and Johnson, 2012). In DFs, restoration treatments may reduce the potential for future carbon loss due to wildfire (Agee, 1996; Stephens et al., 2012a). They may also reduce drought stress in dense forests and increase the resistance of trees to insects and disease (Churchill et al., 2013). So, while the relative reduction of ecosystem carbon stocks is similar across MFs and DFs, the ecological trajectories initiated by restoration treatments may be quite different.

MFs potentially store more C than any other forest (Hudiburg et al., 2011; Mitchell et al., 2009). The forested area of western Washington and Oregon could sequester considerably more carbon if management strategies allowed forest ecosystems to return closer to the carbon stores found in old-growth conditions (Smithwick et al., 2002). Furthermore, the high productivity and long time interval between natural disturbance events in MFs increases the likelihood that a theoretical maximum C stock could be achieved (Hurteau and North, 2010). However, large portions of forest in North America (including MFs) are in some stage of regrowth – following wildfire, harvesting, or other disturbance – and carbon sequestration estimates generated from old-growth forests are not likely to be sufficiently representative for use in regional forest management

(Chen et al., 2004). Thinning in MFs following previous harvests or in plantations may promote the development of old-growth structures on parts of these landscapes (Franklin and Johnson, 2012). In MFs, managers must carefully consider the tradeoffs between increased carbon storage and the ability of thinning to achieve alternative ecological objectives such as enhancing structural complexity.

In DFs, large, high-severity fires have the potential to release large amounts of C that has accumulated in both aboveground and belowground C pools (Breshears and Allen, 2002; Hurteau et al., 2008; Hurtt et al., 2002; Kashian et al., 2006). High severity fires may be the biggest threat to large landscapes in western North America and are linked to forest fragmentation, wildlife habitat availability, erosion rates and sedimentation, post-fire seedling recruitment, carbon sequestration, and other ecosystem properties and processes (Breshears and Allen, 2002; Miller et al., 2009; Williams and Baker, 2012). DFs in our review experienced similar reductions in C pools as MFs, which suggests that inherent differences in productivity between these forest types were not able to overcome the initial carbon debt incurred with thinning. However, the reduction in forest C from thinning DFs comes with the substantial tradeoff of reduced fire risk. For example, Mitchell et al. (2009) found consistent reductions in fire severity with the implementation of fuel treatments in Pacific Northwest forest ecosystems.

4.3. Restoration Effects Over Temporal and Spatial Scales

The lack of recovery of carbon stocks over time is surprising given that thinning stimulates the growth of the residual trees and can reduce their mortality. Effect sizes from simulation studies suggest that regeneration of thinned areas and increased growth of remaining trees did not compensate for the lost C and reduced NPP due to restoration treatments. It is important to note, however, that these longer-term results are almost entirely driven by simulation-based studies; there is very little empirical data documenting treatment effects after 25 years.

Spatial scale of analysis emerged as an important predictor of treatment effect size for aboveground C but not for belowground or total C (Table 4; Supp. Figure 5). This may be attributed, in part, to the predominance of studies conducted at the stand-level (Supp. Figure 3). With more data from larger scale studies, we may anticipate *less* of an overall treatment effect than observed for stand-level or watershed-level studies. Some larger scale studies compute C metrics across heterogeneous study areas or regions that include treated and untreated stands (Ager et al., 2010; Campbell and Ager, 2013; Chiono et al., 2017). This inclusion of untreated areas may mute a treatment effect that would appear stronger at finer spatial scales.

Using a broader spatial scale to examine the effects of restoration on forest C may, in fact, be most appropriate, especially in dry forests: fire-prone landscapes have traditionally been highly structurally heterogeneous at multiple spatial scales (Perry et al., 2011; Williams and Baker, 2012) and the effects of restoration—and any subsequent wildfire—would likely maintain this heterogeneity. Thus, a full accounting of restoration effects on forest C should incorporate the mosaic of treated and untreated areas that may only be captured at larger spatial scales. As stand development proceeds and disturbances occur, this spatial mosaic shifts over time (Pickett and White, 1985; Turner et al., 1993), further highlighting the importance of tracking treatment effects for longer periods of time and at multiple spatial scales.

4.4. Choice of Counterfactual

The choice of baseline for comparison is important in understanding the direction and magnitude of forest management effects. Comparison to pretreatment values can provide valuable information about the changes that result from restoration treatments but fail to account for forest growth and the reallocation of C between pools that would have taken place in the absence of treatment, especially greater net primary productivity (NPP) of dense, untreated forests. While thinning can stimulate individual tree growth (Agee, 1996; Kolb et al., 2007; Peterson et al., 1994), the overall aboveground forest biomass is higher in untreated forests for at least several decades after treatment (Figure 5). Comparison to control plots is preferable because it integrates the trajectories of forest growth in the treated and control areas, assuming that the initial conditions are the same for these areas. However, this assumption is considerable – in several studies recorded in this analysis, the pre-treatment difference between control and treated areas was greater than the subsequent change due to treatment. This may be especially problematic in purely retrospective studies that lack pretreatment data to verify or correct for different initial conditions.

Ideally, pretreatment data should be gathered for both treatment and control stands to allow for complete Before-After Control-Impact (BACI) analysis to account for both types of differences (Conquest, 2000; Smith, 2013). However, this remains a major limitation in much of the forest C literature.

4.5. Fire suppression

The entire study area of western North America has been treated by fire suppression for the past 100+ years, as well as a mosaic of other post-settlement management strategies (Williams and Baker, 2012). In areas where fire suppression has been successful, which includes most of the empirical studies in this review, the C levels observed in control plots could represent a higher end of the historical range of variation in ecosystem C. Especially in dry, ponderosa pine dominated forests, the biomass accumulated in untreated controls left untouched by wildfire for many decades will be much higher than historical norms (Boerner et al., 2008; Stephens et al., 2012b).

4.6. Forest Attributes Moderate Response

Seral status, fire resistance, and shade classes altered different aspects of the forest C response to treatment. Seral status only significantly altered aboveground C, while shade tolerance only altered belowground C response (the primary difference between these two classifications is Douglas-fir and sugar pine, which were classified as early seral trees but medium in shade tolerance). Fire resistance altered both belowground and aboveground C responses, but no effect of any attribute was significant for total C.

In addition to fuel accumulation, decades of fire suppression has also altered forest composition, particularly allowing shade tolerant, late-seral species like true firs (*Abies*) to increase relative to early seral species like ponderosa and Jeffrey pine (Parsons and DeBenedetti, 1979; Williams and Baker, 2012). At least in terms of the response of forest C to thinning and prescribed fire, our results suggest that this shift in composition to include late seral species could reduce C loss relative to pure early-seral forests. Forests dominated by fire resistant trees like Douglas-fir, ponderosa pine, and Jeffrey pine saw greater declines in aboveground C following treatment than did forests with a mix of high and low tolerance species. This may reflect the reference conditions that provide targets for the restoration treatments, and the greater deviation of these forests from those reference conditions. In other words, it may be that the treatments in these forests were designed to remove more C such as by thinning more trees.

4.7. Key gaps in research

The small number of empirical studies measuring response beyond 25 years is not surprising but nonetheless is a major shortcoming of the existing literature. Long-term ecological research is extremely important, especially considering the lifespan of trees and the multi-decadal legacies of forest management and repeated fires on ecosystem properties. Most (89%) of the effect sizes in our dataset calculated over periods of more than 75 years are from simulation studies, which serve an important purpose but carry with them inherent uncertainties and assumptions. For example, the STANDCARB model (Harmon et al., 2009), which underlies several predicted effect sizes in this dataset, aggregates forest carbon into living, detrital, or stable pools, but makes no claim to represent the actual mechanisms that underlie nutrient recycling or soil carbon storage which profoundly impact the productivity of future forests. Simulations are necessarily simplifications of real systems; consequently, they are always wrong but sometimes useful (Box and Draper, 1987), and their utility extends only so far as their underlying assumptions hold true. While we observed significant interactions between treatment effects and study type for total C and between study type and time for aboveground C (Table 4; Figure 5; Supp. Figure 3), these differences do not justify either discounting or validating the accuracy of forest ecosystem C simulations.

Soil C is considerably underrepresented in the literature examining restoration effects. Large quantities of carbon are stored in soil, including in subsurface horizons (Harrison et al., 2011, 2003; Jobbagy and Jackson, 2000). Globally, there is more C stored in soils than in all vegetation and the atmosphere, combined (Schlesinger and Bernhardt, 2012). Furthermore, 36% of soil organic C is found below 1 m depth (Jobbagy and Jackson, 2000). However, the average soil sampling depth across all belowground C effect sizes in this review was 15 cm, and 41% of the belowground C effect sizes examined only surface litter and duff. This depth of sampling is inadequate to capture the soil C pool. For context, a study of 36 soils across the coastal Pacific Northwest determined that the litter and duff accounted for only 5% of total soil C to 3 m, and the litter plus top 20 cm of soil accounted for less than 30% of total soil C (James et al., 2014). Nor is it safe to assume that deep soil C will be stable in response to treatment; Gross et al. (2018) found significant reduction (25%) in soil C 40 years after forest thinning in a northern Oregon forest with the majority of loss occurring below 20 cm depth. More fully accounting for soil C would increase the size of this stock and potentially alter the dynamics seen in surface soil.

However, while surface soil may be expected to respond more quickly to disturbance, forest harvesting and associated soil disturbances can also destabilize deep soil organic matter with legacy effects extending at least 50 years (James and Harrison, 2016). Losses in subsurface C can offset gains in surface soil over decadal timescales (Mobley et al., 2015), and alterations to the input rates of fresh C are a major control over the long-term stability of deep soil C (Fontaine et al., 2007). Deep soils also respond substantially to warmer temperatures, with subsoil (> 30 cm) accounting for 10% of the response of soil respiration to 4°C warming (Hicks Pries et al., 2017). The assumption that only surface soil C changes in response to forest management is simply untrue and potentially misleading. Studies that report soil C gains in response to thinning treatments in our review frequently only sample the litter layer, with no accounting for the priming effect this can have on subsurface soil C decomposition (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010; Kuzyakov et al., 2000). The lack of deep soil sampling in the literature available for this review represents a substantial gap in knowledge.

4.8. Exported carbon

Our assessment focused on in-forest carbon stocks and did not track the fate of carbon exported from the system. Restoration treatments can directly result in carbon export in several ways, including the removal of merchantable wood following thinning and emissions from prescribed fires or from burning slash piles. Emissions are also released from the equipment used in the treatment process (Stephens et al., 2009). Furthermore, treatment residues tend to be smaller and therefore decompose more quickly than naturally recruited dead organic matter, releasing further carbon (Janisch et al., 2005). This analysis also did not consider the surface and subsurface transfer of carbon through hydrologic pathways. A recent analysis at the watershed scale suggests that upwards of 159 kg C ha^{-1} of organic and inorganic carbon is transported out of an undisturbed moist forest ecosystem; this value represents 6% of terrestrial net ecosystem production (Argerich et al., 2016). No further studies have measured aquatic carbon loss pathways under restoration treatments, but the proportional loss may be larger given our finding that restoration reduces total carbon accumulation over time.

Wood products represent a loss of carbon from the forest perspective, but the carbon in these products remains sequestered for a period of time depending upon the particular product. Because solid wood products are not susceptible to wildfire, pests, and pathogens, they represent a stable carbon pool that may hold carbon for up to 100 years (Berrill and Han, 2017) to 250 years (Harmon et al., 2009). Harvest removals for bioenergy represent a middle ground between the immediate emission of C from fire and the longer-term stability of wood products (Creutzburg et al., 2016). Restoration thinning treatments create less merchantable timber than conventional harvest practices, but may recover the difference over time through steady, sustained yield (Berrill and Han, 2017). A full life-cycle analysis of carbon flux in and out of forest pools is needed to understand the ultimate outcomes for atmospheric carbon levels.

4.9. Wildfire

A primary motivation for restoring fire-prone forest systems is to reduce fuel loads and thereby minimize the risk and/or severity of future wildfires (Prichard and Kennedy, 2014; Yocom Kent et al., 2015). Wildfire can have immediate and enduring effects on forest C: for example, C is emitted directly to the atmosphere during combustion (North et al., 2009) and more gradually from post-fire decay (Campbell et al., 2016). At the same time, C is fluxed into recalcitrant C pools like charcoal (DeLuca and Aplet, 2008) or sequestered over time in post-fire regrowth (Loudermilk et al., 2014). Thus, our understanding of the long-term C dynamics associated with restoration is incomplete unless we also consider how wildfire plays out on restored landscapes.

Our comparisons suggest that wildfire reduces the loss of aboveground C due to treatment and that these C stores may be restored in the long run (Figure 3). It is important to note that these patterns are largely based upon simulations as few empirical studies reported how treatment effects on C were moderated by wildfire. Several simulations suggest that *in situ* C storage benefits of restoration may *only* be realized in the case of wildfire, while others find no such effect; these differences highlight that treatment type and time-frame are important drivers. For example, Hurteau and North (2009) reported that C storage increased in some treated areas if wildfire was included in their 100-year simulations but decreased if it was not included. On a shorter time frame (eight years), Vaillant et al. (2013) reported that treatments caused a net reduction in aboveground C relative to control but that simulating a wildfire minimized this reduction. On the other hand, Reinhardt and Holsinger (2010) did not find an increase in post-wildfire C after a 95-year simulation: some drier forest types had little difference between treated and untreated stands while treated stands in moister forests had less C than untreated stands. This range of responses suggests that conclusions regarding *in situ* C may be highly site-specific and depend on simulation duration and/or parameters. The resolution at which forest type or species traits are examined will matter, too: aggregating across studies, little difference in post-treatment and post-wildfire C was observed between broad forest types (Fig. 9), but species traits (e.g., fire resistance) may dictate the net treatment effect on some C pools (Supp. Fig. 3).

In all cases, simulation results will be sensitive to multiple facets of the simulated fire regime and the wildfire events themselves. For example, over 50-year simulations, Winford and Gaither (2012) found that whether treated areas were C sources or sinks depended on the fire return interval; the break-even point was a fire return interval of 31 years. Krofcheck et al. (2017) reported that fuels treatments stabilized C stocks in the presence of wildfire only under extreme fire weather conditions (which increased fire severity and size). Furthermore, emissions associated with burning—whether prescribed or as wildfire—are also a critical piece of the C equation that may offset apparent gains of *in situ* C storage. Several studies, for example, showed via simulation that prescribed fires to reduce fuels also reduced direct C emissions from wildfires immediately following treatment, but that emissions from the prescribed fire exceeded the reductions in wildfire emissions (Ager et al., 2010; Chiono et al., 2017). Longer simulations that incorporate the probabilistic occurrence of wildfire, various burning conditions and emissions, and post-fire stand development will help isolate the sensitivities of post-treatment and post-wildfire C storage (Ager et al., 2010). Furthermore, the spatial heterogeneity with which treatments and wildfires play out—and the spatial scope at which C effects are examined—will affect the net C equation. Campbell and Ager (2013) point out that an increase in treatment application rate may reduce area burned, but may not affect C stocks to an appreciable degree because the area burned may represent only a small fraction of the broader landscape under consideration. In sum, even if the interaction between treatments and wildfire decrease the loss in C due to treatment, the actual area burned in wildfire—and thus able to realize the benefits of treatment related to C storage—is relatively small compared to the entire treated, and mostly unburned, landscape in these simulations (Ager et al., 2010; Campbell and Ager, 2013; Chiono et al., 2017; Spies et al., 2017).

Realistically simulating where, when, and how wildfire will occur is challenging because of the stochastic nature of the disturbance itself, changing climatic conditions that may affect fire regimes, and an incomplete understanding of how restoration affects wildfire behavior in the long term (Campbell and Ager, 2013; McKenzie et al., 2004). In the face of these uncertainties, researchers can make C projections more robust by simulating across a range of future climate and wildfire scenarios and identifying how sensitive projections are to key parameters (e.g., fire return interval and fire weather) (Krofcheck et al., 2017; Loudermilk et al., 2017; Winford and Gaither, 2012). Furthermore, as on-the-ground evidence accumulates, we can more accurately parameterize fire behavior models, emissions models, and post-fire recovery models to refine C projections for restored landscapes. Two of the empirical studies that we reviewed report such evidence following the 2002 Biscuit Complex Fire in SW Oregon, which burned several existing experimental plots (Bormann et al., 2015; Homann et al., 2015). Eight years post-fire, thinned plots had less aboveground and total carbon than unthinned plots; this difference exceeded the difference between thinned and unthinned *unburned* plots. The researchers attribute this substantial reduction in C to high levels of fine wood from thinning, which fueled more intense fire and mortality in treated plots (Bormann et al., 2015). This suggests that intense wildfire risk may diminish with time since treatment as fine fuels decompose.

Although the studies referenced above are intriguing, they are uncommon. Few studies in our dataset – particularly of the empirical studies – examined wildfire. There are clear research needs in terms of characterizing the interactions between fuels treatments and wildfire and assessing the enduring effects on forest C. This is particularly true in light of the spatial heterogeneity of forest recovery, which is strongly controlled by endogenous, stand-level processes (e.g., seed delivery; Haire and McGarigal 2010) as well as external constraints (e.g., post-fire climatic conditions; Harvey et al. 2016). Accordingly, treated areas that recover rapidly post-fire are more likely to have smaller long-term losses of C due to treatment than areas that experience limited or protracted recovery due, for example, to limited seed source (League and Veblen 2006). Thus, the likelihood that wildfires will occur across many of these forest systems may temper some of the C lost from restoration treatments, but the spatial heterogeneity of post-fire recovery will be an important consideration in forest management.

4.10. Limitations of our review process

Variability across the articles we reviewed compelled us to make several simplifying assumptions and categorizations throughout our review process, as did the paucity of results reflecting some levels of our covariates (e.g., there were few studies conducted at the ecoregion level). Our mixed effect modeling framework accounts for the distinctness of each article and the inclusion of multiple effect sizes from some articles. Nonetheless, variability across articles in C sub-pools, treatment intensities, counterfactual conditions, wildfire effects, simulation choice, and spatial and temporal scales may be obscured in, and confound, our results. For example, the aboveground, belowground, and total C pools do not always include the same sub-pools because of inconsistencies among study methodologies in terms of which sub-pools were measured and how they were reported (Figure 2). We also did not account for treatment objectives, intensity (e.g., percent of basal area removed) or frequency. These differences can have long-term implications for C recovery (D'Amore et al., 2015; Hurteau et al., 2011).

There are also caveats to our categorization of forest attributes. Because our study inherits the forest types that are reported in the literature, the classes are unbalanced and are likely a biased sample. Furthermore, reporting of canopy trees is not detailed in several studies, leading to the possibility of important species missing for our forest attribute categorization. However, there are important ecological differences in the trees represented by each of these groups that could impact the resistance and/or resilience of a forest to human disturbances.

Finally, this review inherently propagates any uncertainties in and limitations of the studies themselves. For example, in some studies the treated areas had different initial conditions than the corresponding control areas. While our geographic scope covered the western United States, studies on this topic tended to concentrate in a few ecoregions and forest systems.

These limitations suggest that our findings ought to be applied to management decision-making with caution and that inferences ought not to be drawn beyond the range of forest and treatment types we examined. Nevertheless, our review underscores the importance of synthetic science in understanding management outcomes and highlights critical data gaps in the forest C literature. More consistent, standardized reporting of C metrics, sub-pools, and experimental errors (sample size and standard deviation) would greatly facilitate researchers' abilities to conduct such syntheses (e.g., via meta-analyses).

5. Conclusions & Considerations

A systematic review of the literature related to ecological restoration treatments in forests of western North America indicates that treatments cause reductions in forest carbon. Surprisingly, we found no difference in response to thinning between moist and dry forests. However, critical knowledge gaps remain in terms of the impact of forest restoration treatments on carbon cycling at long timeframes, at large spatial scales, and within deeper soil depths. Most studies focused on stand-scale measurements, and C accounting at this level almost certainly obscures the tremendous heterogeneity of forest stand conditions, stages of development, and disturbance regimes that affect C storage.

Given those caveats, our review did uncover several patterns that raise questions about the relationship between restoration management and carbon dynamics. Thinning and thinning & fire treatments most strongly affect the aboveground C pool, while prescribed fire impacts the belowground pool. However, post-treatment wildfire is an important moderator – when it occurs, the relative loss of aboveground C due to treatment is reduced. Detailed analyses of C sub-pools would be valuable but will require more consistent methodologies for measuring and reporting these sub-pools. To fully quantify the relationship between ecological restoration treatments and net carbon flux from forest landscapes, a complete life cycle assessment (LCA) must be made. The results from this systematic review represent only the within-forest portion of LCA, without considering the out-of-forest fate of wood products, eroded sediments, and dissolved organic matter. Furthermore, the probability, severity, and frequency of wildfire must be balanced against losses of carbon due to treatment to gain insight into the fate of carbon cycling across large spatial scales and long timeframes. The impact of climate change on the behavior and frequency of wildfire and forest health may dynamically shift forest management priorities in both time and space (Hurteau, 2017; Spies et al., 2017). As managers work to prioritize where, when and whether to apply restoration treatments, they must carefully consider the tradeoffs between carbon cycling, ecological objectives, and social priorities.

6. Data Availability Statement

All data used in this study have been made available in the article text, appendices and supplemental materials.

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9. Author Contributions

J.N.J. wrote the paper with major contributions and input from all authors. J.N.J. and J.D.B. analyzed the data with contributions from C.D.K. and discussion with all other authors. J.D.B, D.E.B., R.D.H., and C.D.K. conceived the initial intent for this project and framed research questions. All authors contributed critically to the development of the review protocol, discussed results and implications, provided input on multiple drafts of this work, and gave approval for publication of the final manuscript.

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Yocom Kent, L.L., Shive, K.L., Strom, B.A., Sieg, C.H., Hunter, M.E., Stevens-Rumann, C.S., Fulé, P.Z., 2015. Interactions of fuel treatments, wildfire severity, and carbon dynamics in dry conifer forests. For. Ecol. Manage. 349, 66–72. doi:10.1016/j.foreco.2015.04.004

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11. Tables

Table 1. Initial search criteria used during systematic review. Keywords were used to search the CAB and Web of Science databases. Searches using the Boolean operator * find all endings of the preceding word.

Criterion	Keywords
Forest Type	Forest*, Ponderosa pine, Douglas-fir, western hemlock, *Pinus ponderosa*, *Pseudotsuga menziesii, Tsuga heterophylla*, mixed conifer
Intervention	Forest restoration, thin*, mechanical treatment, pre-commercial thin, prescri* fire, prescri* burn*, control* burn, wildfire, fire suppression, fuel management, forest management
Location	Pacific Northwest, Rockies, Cascades, Coast Range, Washington, WA, Oregon, Idaho, ID, Montana, MT, California, CA, Arizona, AZ, New Mexico, NM, Nevada, NV, Utah, UT, Colorado, CO, Wyoming, WY, British Columbia, North America, western United States, western Canada
Carbon	Carbon, CO_2, Total C, forest carbon, climate change mitigation, carbon balance, carbon dynamics, carbon sequestration, carbon sink, net ecosystem production, carbon budget, soil C*, soil organic matter, carbon flux, belowground carbon, aboveground carbon, belowground biomass, aboveground biomass, emissions

Table 2. Ecosystem characteristics and moderating factors included in our predictive models of treatment effect size.

Moderator	**Description**		
Treatment	Prescribed Fire; Thinning; Thinning & Fire		
Counterfactual	Control; Pretreatment; Post-Wildfire		
Spatial Scale	Stand: 0-100's of ha; Watershed: 1,000's to 10,000's of ha; Landscape: 100,000's of ha; Ecoregion: 1,000,000's of ha		
Wildfire	Present (included in effect size); Absent (not present, or present but excluded in effect size calculation)		
Time Since Treatment	Continuous (years); Later grouped into four bins: ≤5 years, 5-25 years, 25-75 years, and >75 years		
Fire Regime (Barrett et al., 2010)	Fire Regime Group I: 0-35 year frequency and low severity; Fire Regime Group II: 0-35 year frequency and high severity; Fire Regime Group III: 35-100+ year frequency and mixed severity; Fire Regime Group IV: 35-100+ year frequency and high severity; Fire Regime Group V: 200+ year frequency and high severity		
Study Type	Empirical; Simulation		
Forest Type	Moist Forest; Dry Forest		
Forest Attributes (Defined by species reported as dominant/co-dominant in canopy) [a]	Seral Status	Early: Mid: Late:	DF, JP, LP, PP, IC, SP, WL Combination of early and late seral species RF, WH, WF, WRC
	Fire Resistance	High: Medium: Low:	DF, JP, PP, WL IC, SP, or combination of high and low LP, RF, WF, WH, WRC
	Shade Tolerance	High: Medium: Low:	IC, RF, WF, WH, WRC DF, SP, or combination of high and low JP, LP, PP, WL
	Drought Tolerance	High: DF, JP, LP, PP, IC Medium: SP, or combination of high and low Low: RF, WF, WH, WL, WRC	

[a] Key for species: DF = Douglas-fir, IC = incense cedar, JP = Jeffrey pine, LP = lodgepole pine, PP = ponderosa pine, RF = red fir, SP = sugar pine, WF = white fir, WH = western hemlock, WL = western larch, WRC = western redcedar.

Table 3. Mean percentage change relative to control (±SD) across all timeframes for three restoration treatments and the aboveground, belowground, and total forest carbon pools. Results from empirical and simulation studies are reported separately. Average time since treatment is 10 (±21) years for empirical and 112 (±62) years for simulation studies.

	Prescribed Fire	*n*	Thinning	*n*	Thinning & Fire	*n*
Empirical						
Aboveground C	-13% (±24%) * a	22	-28% (±21%) * b	41	-39% (±18%) * b	22
Belowground C	-20% (±31%) * j	41	3% (±34%) k	54	-12% (±38%) k	37
Total C	-14% (±22%) * y	13	-23% (±22%) * y,z	28	-33% (±19%) * z	16
Simulation						
Aboveground C	-8% (±27%)	3	-28% (±30%) *	22	-17% (±16%) *	11
Belowground C			13% (±14%)	3	2%	1
Total C	-8% (±4%) *	6	-14% (±13%) *	20	0% (±16%)	15

Effect sizes followed by a * are significantly different from 0 (two-sided t-test, $p < 0.05$). Within each row (C pool), interventions with different lowercase letters are significantly different from one another at $\alpha = 0.05$.

Table 4. Results of back-fitted mixed effects models showing random and fixed effects that moderate the response of forest C to treatment. Paper ID was modeled as a random effect; all other terms were coded as fixed effects. Forest attributes were evaluated in a second back-fitting step after other significant factors were identified. Bolded terms are significant at $\alpha = 0.05$. Factors eliminated from final models appear in light grey. Terms are defined in Table 2. All analyses are based on effect sizes calculated relative to control.

Aboveground C						
	Random Effects	DF		*LRT* [a]	*p-value (Chi-sq)*	
	Paper ID	1		0	1	
First Stage	Fixed Effects	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Treatment	**2**	**109**	**6.8**	**0.002**	**no**
	Study Type	1	110	2.8	0.10	no
	Spatial Scale	**3**	**110**	**4.5**	**0.005**	**no**
	Fire Regime Group	3	110	0.3	0.83	yes
	Forest Type	1	107	1.7	0.18	yes
	Wildfire	**1**	**110**	**5.7**	**0.02**	**no**
	Time	1	110	2.6	0.11	no
	Treatment : Study Type	2	108	0.7	0.49	yes
	Wildfire : Study Type	**1**	**110**	**4.4**	**0.04**	**no**
	Time : Study Type	**1**	**110**	**5.5**	**0.02**	**no**
Second Stage	Fixed Effects	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Stand Attributes					
	Seral Status	**1**	**16**	**18.0**	**0.0006**	**no**
	Shade Tolerance	2	107	0.03	0.96	yes
	Fire Resistance	**1**	**105**	**4.3**	**0.04**	**no**
	Drought Tolerance	1	108	0.5	0.49	yes
	Seral Status : Study Type	**1**	**24**	**10.5**	**0.004**	**no**
Belowground C						
	Random Effects	DF		*LRT* [a]	*p-value (Chi-sq)*	
	Paper ID	**1**		**15.4**	**0.00009**	
First Stage	Fixed Effects [c]	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Treatment	**2**	**131**	**6.0**	**0.003**	**no**
	Study Type	1	77	1.0	0.32	yes
	Spatial Scale	2	42	3.0	0.06	yes
	Fire Regime Group	2	58	0.8	0.45	yes
	Forest Type	1	51	1.4	0.24	yes
	Wildfire	1	130	1.4	0.23	yes
	Time	1	64	0.2	0.65	yes
	Treatment : Study Type	1	77	0.4	0.54	yes
	Wildfire : Study Type	1	98	0.7	0.42	yes
	Time : Study Type [c]					
Second Stage	Fixed Effects	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Stand Attributes					
	Seral Status	1	44	0.1	0.83	yes
	Shade Tolerance	**2**	**92**	**9.0**	**0.0002**	**no**
	Fire Resistance	**1**	**89**	**7.1**	**0.009**	**no**
	Drought Tolerance	1	35	0.0	0.90	yes
	Fire : Shade Tolerance	1	53	0.6	0.46	no
Total C						
First Stage	Random Effects	DF		*LRT* [a]	*p-value (Chi-sq)*	
	Paper ID	**1**		**4.3**	**0.03**	
	Fixed Effects	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Treatment	2	87	1.0	0.35	no

	Study Type	**1**	**24**	**12.1**	**0.002**	**no**
	Spatial Scale	3	22	1.4	0.26	yes
	Fire Regime Group	3	39	0.8	0.51	yes
	Forest Type	1	51	1.9	0.17	yes
	Wildfire	1	83	0.3	0.56	yes
	Time	1	23	0.3	0.60	yes
	Treatment : Study Type	**2**	**87**	**4.2**	**0.02**	**no**
	Wildfire : Study Type	1	81	1.1	0.29	yes
	Time : Study Type	1	29	2.5	0.12	yes
Second Stage	Fixed Effects	DF	Denom. DF [b]	*F*	*p-value*	Eliminated?
	Stand Attributes					
	Seral Status	1	54	0.8	0.38	yes
	Shade Tolerance	2	35	0.7	0.49	yes
	Fire Resistance	2	41	0.4	0.67	yes
	Drought Tolerance	1	20	0.1	0.80	yes

[a] Likelihood ratio test statistic
[b] Denominator degrees of freedom calculated with the Satterthwaite method
[c] Insufficient samples for test

12. Figure Captions

Figure 1: Flow chart showing systematic review process, including how inclusion/exclusion criteria (Table 1) were used to filter the articles returned by our literature searches down to the final 73 articles included in our systematic review.

Figure 2: Heatmap showing the presence or absence of different C sub-pools (y-axis) in each article that reports aboveground, belowground, or total C. Within each C pool, each article is reported as a column. Black bars show when a sub-pool is present for all effect sizes in the article; gray bars show when only a portion of effect sizes in an article include a sub-pool; white bars show absence of data.

Figure 3: Violin plot showing the difference in the response of forest C pools (rows) to treatment when reported in empirical or simulation studies (columns) and when wildfire was present or absent after treatment. Filled black points are mean effect sizes (vertical black lines, ± 1 standard deviation). Smaller points are individual effect sizes calculated from published studies and are jittered horizontally to better show density of individual effects. In simulation studies, treated stands show significantly less aboveground C loss relative to control after wildfire than when no wildfire occurred (Wildfire $F = 4.8$, $p = 0.03$; Wildfire : Study Type $F = 4.2$, $p = 0.04$; Table 4). Average time since treatment for aboveground C simulation studies is 88 (±24) years when wildfire is absent and 87 (±22) years when it is present.

Figure 4: Locations of study sites and the average effect size associated with each site. Geographic coordinates were extracted for each effect size comparison. Where no or imprecise coordinates were given, coordinates were assigned based on the site names or other geographic metadata embedded in the site descriptions. Six studies gave no deducible geographic information. See Supplemental data for a complete list of study coordinates. Inset shows the count of study sites per US EPA Level III Ecoregions.

Figure 5: Scatterplot of the percent change in forest C over time since treatment. Symbol shape differentiates study types. Points are colored red when the effect size is calculated after wildfire burned or was simulated to burn through both treatment and control areas. Six points are not shown due to long simulation timeframes (800-1500 years) that obscure the rest of the data if plotted. Blue lines with 95% confidence intervals in grey show the trend over time for each treatment and C pool. There is a significant interaction between time since treatment and study type (Time:Study Type $F = 5.5$, $p = 0.02$), with most empirical results within 25 years since treatment and most simulation results after 75 years since treatment.

Figure 6. Effect of restoration treatments on aboveground, belowground, and total C pools in forests with early or mid/late seral statuses. Violin plot interpretation as in Figure 3. Seral status is a significant predictor of the response of aboveground C to treatment, both as a main effect ($F = 17.6$, $p < 0.0001$) and in interaction with study type ($F = 10.5$, $p = 0.002$). Symbol color and shape distinguish effect sizes from empirical and simulation studies.

13. Figures

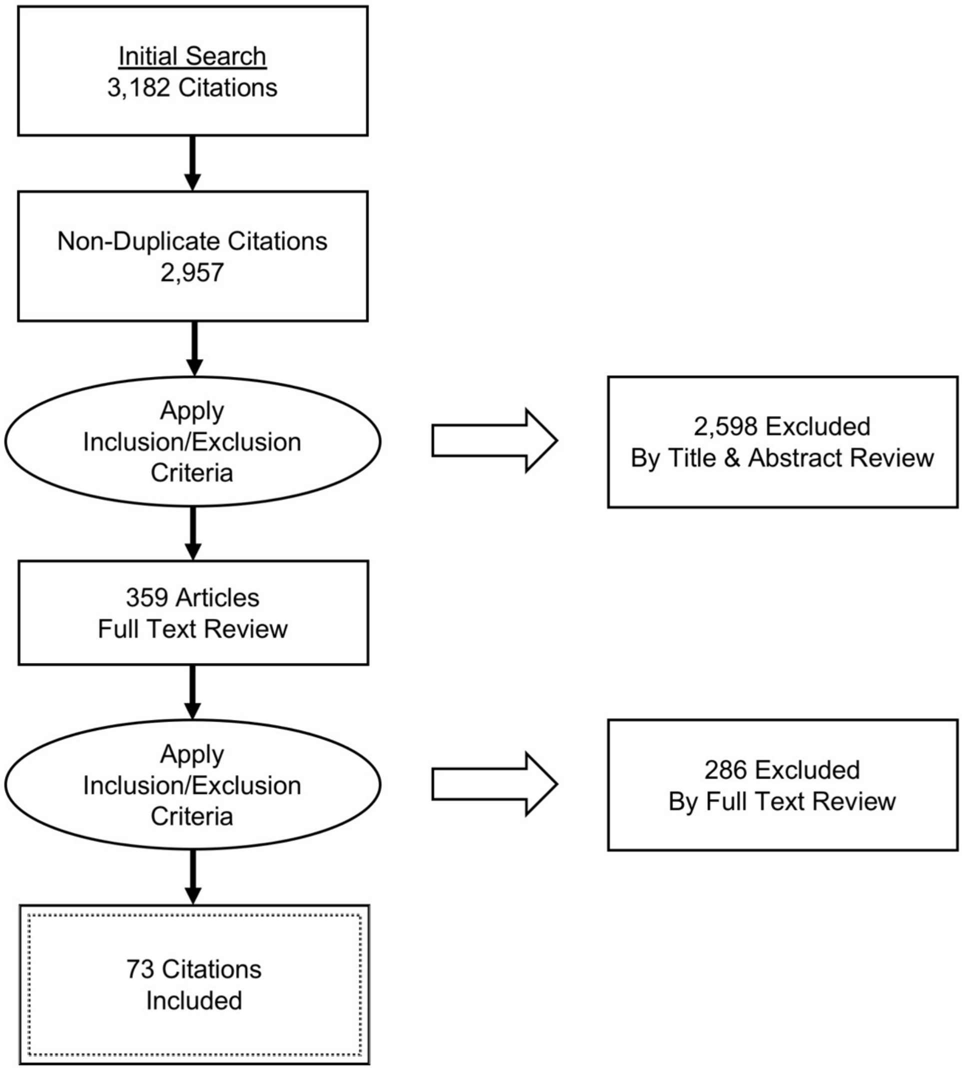


Figure 1.

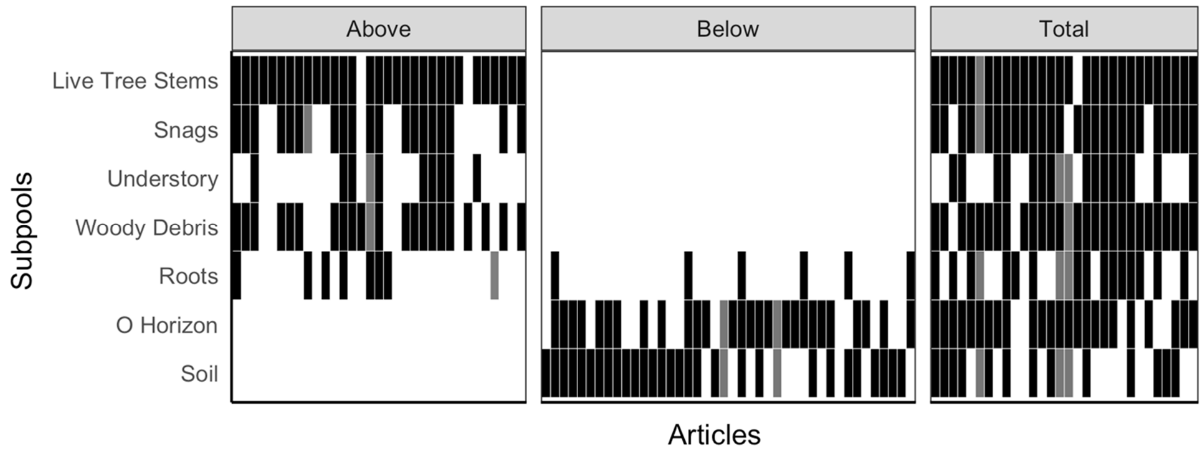
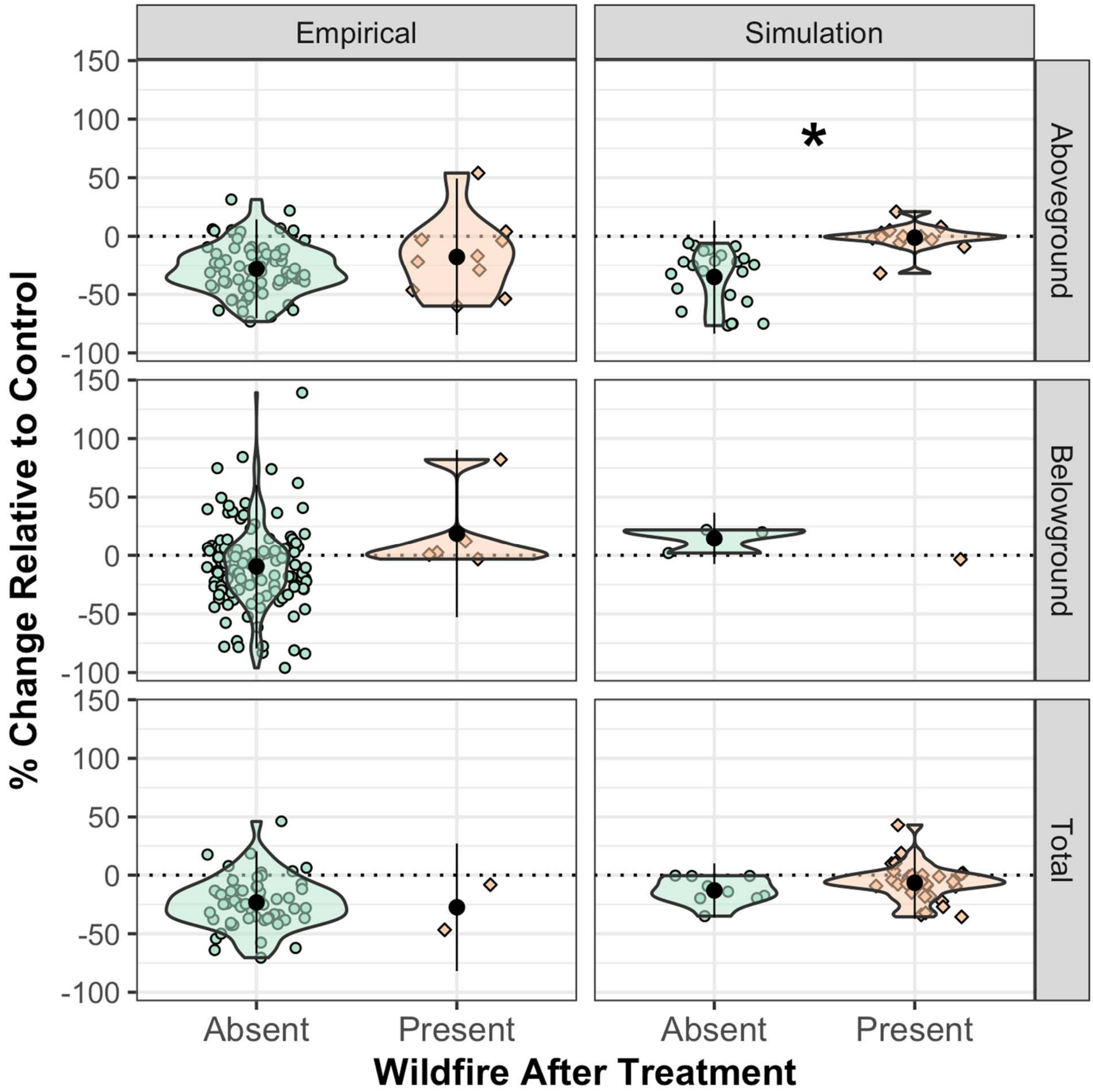

Above
Below
Total
Live Tree Stems
Snags
Understory
Woody Debris
Roots
O Horizon
Soil
Subpools
Articles

Figure 2.



1292
1293 **Figure 3**.
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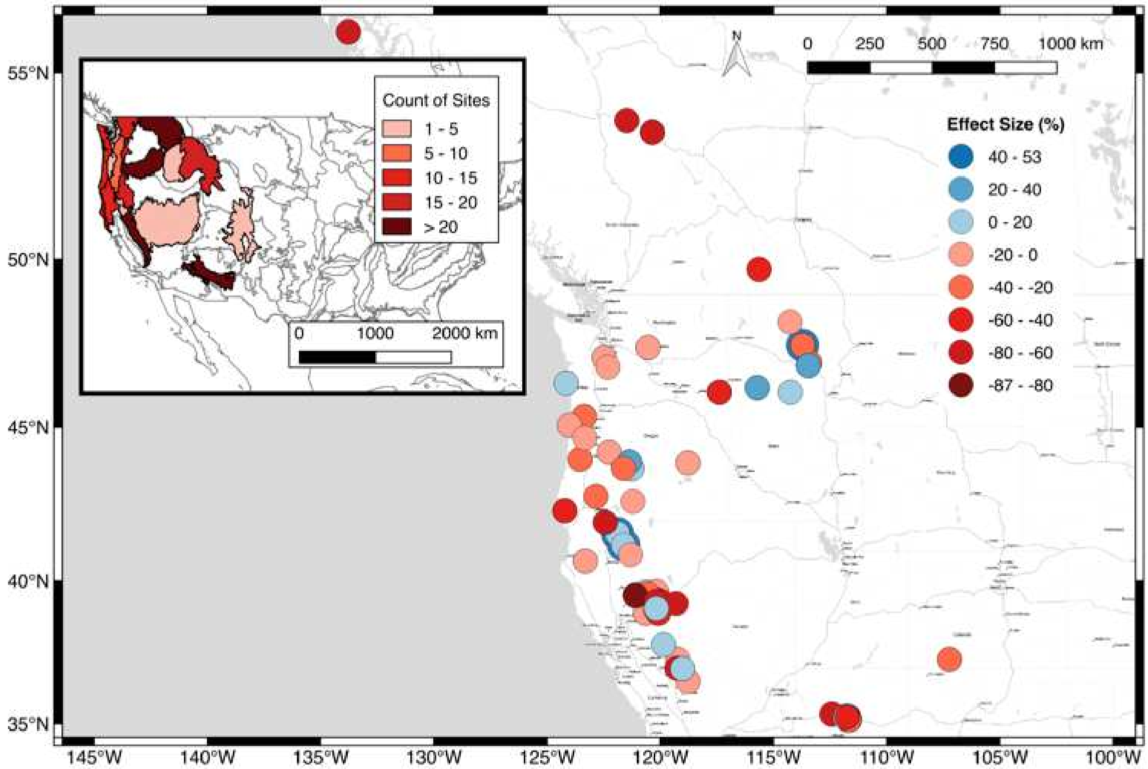

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1297 **Figure 4**.

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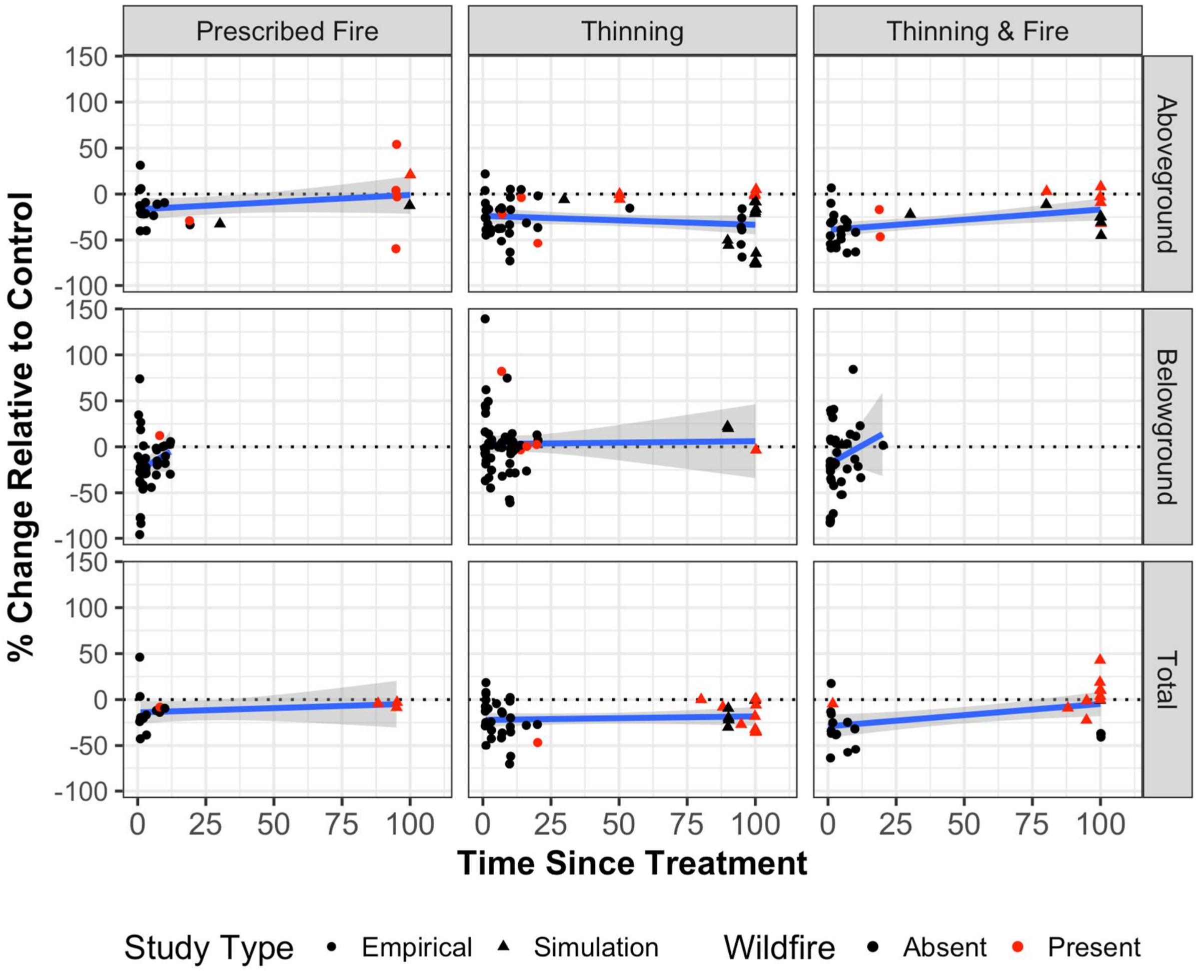

1299

1300 **Figure 5**.

1301

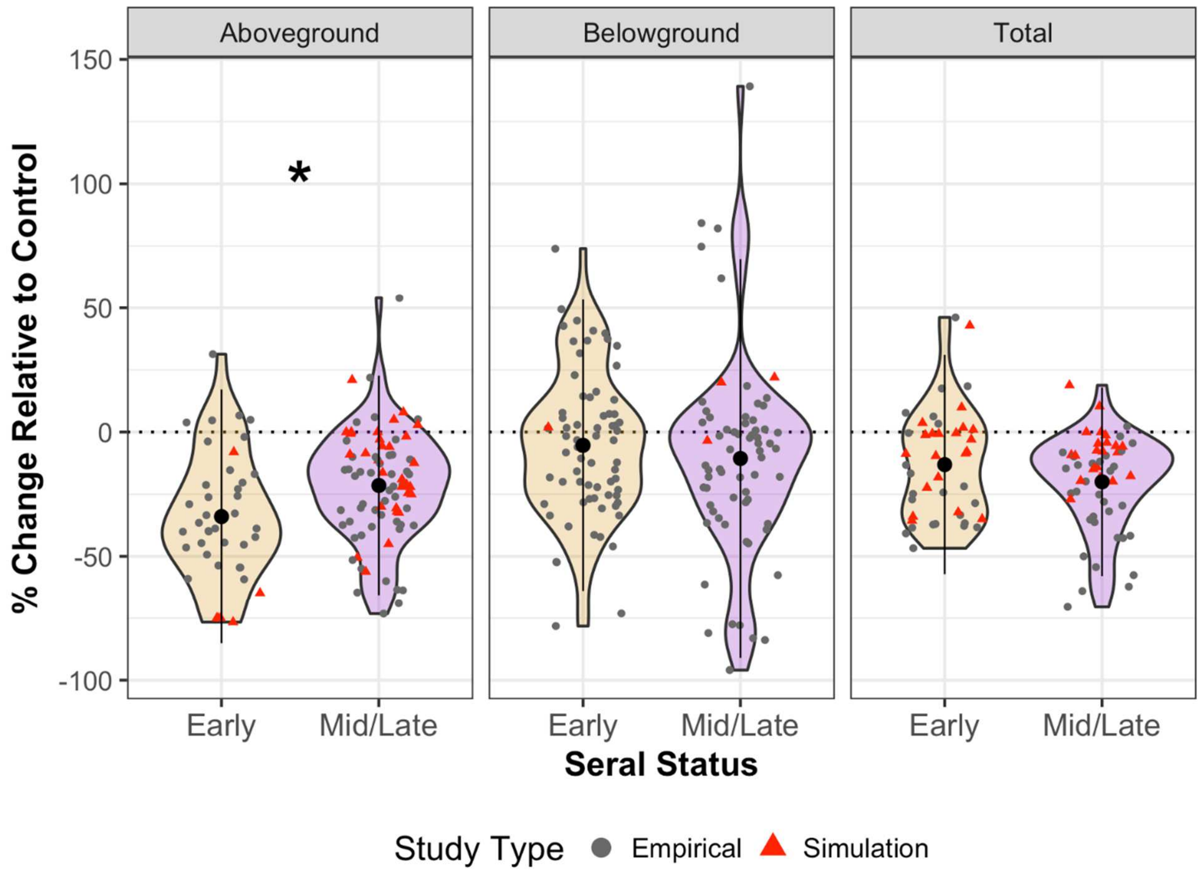
Aboveground
Belowground
Total
150
100
50
0
-50
-100
% Change Relative to Control
*
Early
Mid/Late
Seral Status
Study Type
Empirical
Simulation

Figure 6.

14. Appendices

Appendix 1: Publications providing effect sizes for this review.

Source	***Number of Effect Sizes***	***Dominant / Co-dominant Trees***	***Carbon Pools***[a]	***Interventions***[b]	***Post-Treatment Wildfire***
Ager et al. (2010)	1	PP	T	Th+F	Present
Bagdon and Huang (2014)	6	PP	T	T+F	Absent
Berrill and Han (2017)	6	DF	A	Th	Absent
Boerner et al. (2008)	124	DF, IC, PP, RF SP, WF	A, B, T	Th, F, Th+F	Absent
Bormann et al. (2015)	6	DF	A, B, T	Th	Present & Absent
Burton et al. (2013)	3	DF, WH	A	Th	Absent
Caldwell et al. (2002)	3	JP, PP, RF, WF	B	F	Absent
Campbell et al. (2009)	6	DF, IC, PP, WF	A, B, T	Th	Absent
Campbell and Ager (2013)	4	DF, LP, PP, WF, WL	A	Th+F	Present & Absent
Carlson et al. (2012)	12	IC, JP, LP, RF, SP, WF	A, B, T	Th	Present & Absent
Chiono et al. (2017)	1	DF, IC, PP, SP, WF	T	Th+F	Present
Collins et al. (2011)	6	DF, IC, PP, RF, SP, WF	A	F	Present
Cowan et al. (2016)	2	PP	B	F	Absent
Creutzburg et al. (2016)	8	DF, WH	A, B, T	Th	Absent
Creutzburg et al. (2017)	3	DF, WH	A, B, T	Th	Present
D'Amore et al. (2015)	6	WH, WRC	A	Th	Absent
Deluca and Zouhar (2000)	6	DF, PP	B	Th, Th+F	Absent
Dore et al. (2010)	6	PP	A, B, T	Th	Absent
Dore et al. (2014)	2	DF, IC, PP, SP, WF	B	F	Absent
Dore et al. (2016)	3	DF, IC, PP, SP, WF	A	Th, F, Th+F	Absent
Finkral and Evans (2008)	1	PP	A	Th	Absent
Ganzlin et al. (2016)	6	DF, LP, PP	B	Th, F, Th+F	Absent
Grady and Hart (2006)	2	PP	B	Th, Th+F	Absent
Gundale et al. (2005)	6	DF, PP	B	Th, F, Th+F	Absent
Hamman et al. (2008)	2	IC, JP, PP, WF	B	F	Absent
Harmon et al. (2009)	3	DF, WH	T	Th	Absent
Hart et al. (2006)	1	PP	B	Th+F	Absent
Hatten et al. (2008)	4	PP	B	F	Absent
Homann et al. (2015)	4	DF, SP	B	Th	Present & Absent
Hurteau and North (2009)	22	IC, JP, RF, SP,	A	Th, F, Th+F	Present & Absent

Source	*Number of Effect Sizes*	*Dominant / Co-dominant Trees*	*Carbon Pools[a]*	*Interventions[b]*	*Post-Treatment Wildfire*
		WF			
Hurteau and North (2010)	15	IC, JP, RF, SP, WF	A, B, T	Th, F, Th+F	Absent
Hurteau et al. (2011)	6	PP	A, B	Th+F	Absent
Hurteau et al. (2014)	3	IC, JP, PP, RF, SP	A	Th, F, Th+F	Absent
Hurteau et al. (2016)	6	PP	T	T, T+F	Absent
Hurteau (2017)	1	PP	T	Th+F	Present
Johnson et al. (2008)	2	JP	T	Th	Absent
Johnson et al. (2014)	9	IC, JP, RF, SP, WF	B, T	Th, F, Th+F	Absent
Kantavichai et al. (2010)	1	DF	A	Th	Absent
Kaye et al. (2005)	6	PP	A, B	Th, Th+F	Absent
Korb et al. (2004)	4	DF, PP, WH	A	F, Th+F	Absent
Krofcheck et al. (2017)	2	IC, JP, LP, PP, RF, SP, WF	A	Th, Th+F	Absent
Laflower et al. (2016)	3	DF, WH, WRC	T	Th, F, Th+F	Present
Loudermilk et al. (2014)	2	IC, JP, LP, PP, RF, SP, WF	T	Th	Absent
Loudermilk et al. (2017)	3	IC, JP, LP, PP, RF, SP, WF	T	Th+F	Present
Matsuzaki et al. (2013)	15	WH, WRC	A, B, T	Th	Absent
Miesel et al. (2009)	2	PP, WF	B	Th	Absent
Minocha et al. (2013)	3	IC, JP, RF, SP, WF	B	Th, F, Th+F	Absent
Mitchell et al. (2009)	9	DF, PP, WH, WRC	T	Th, F, Th+F	Present
Moghaddas and Stephens (2007)	3	DF, IC, PP, SP, WF	B	Th, F, Th+F	Absent
Monleon et al. (1997)	3	PP, RF, WF	B	F	Absent
Murphy et al. (2006)	5	JP, WF	B	Th, F	Absent
North and Hurteau (2011)	1	IC, JP, PP, RF, SP, WF	T	Th	Present
North et al. (2009)	12	IC, JP, RF, SP, WF	A, B, T	Th, F, Th+F	Absent
Oneil and Lippke (2010)	1	DF, PP	T	Th	Present
Overby et al. (2016)	3	PP	B	Th, F, Th+F	Absent
Perry et al. (1987)	1	DF	B	Th	Absent
Perry et al. (2012)	3	DF, WH, WRC	B	Th	Absent
Reinhardt and Holsinger (2010)	10	DF, PP, WH, WRC	T	Th, F, Th+F	Present
Roaldson et al. (2014)	4	JP	B	Th, F, Th+F	Absent

Source	*Number of Effect Sizes*	*Dominant / Co-dominant Trees*	*Carbon Pools*[a]	*Interventions*[b]	*Post-Treatment Wildfire*
Ryu et al. (2009)	3	IC, JP, RF, SP, WF	B	Th, F, Th+F	Absent
Schaedel et al. (2016)	1	WL	A	Th	Absent
Sorensen et al. (2011)	12	PP	A, B, T	T	Absent
Spies et al. (2017)	3	DF, IC, LP, PP, RF, SP, WH	A	Th	Present
Stephens et al. (2009)	9	DF, IC, PP, SP, WF	A, B, T	Th, F, Th+F	Absent
Stephens et al. (2012a)	15	DF, JP, IC, PP, RF, SP, WF	B	Th, F, Th+F	Absent
Switzer et al. (2012)	3	DF, WL	B	Th, Th+F	Absent
Trappe et al. (2009)	2	PP	B	F	Absent
Vaillant et al. (2013)	6	DF, IC, JP, LP, PP, RF, SP, WF	A, B, T	F	Present & Absent
Vegh et al. (2013)	4	PP	A	T	Present
Wiechmann et al. (2015)	15	IC, JP, RF, SP, WF	A, B, T	Th, F, Th+F	Absent
Winford and Gaither (2012)	2	DF, IC, PP, SP, WF	A	Th	Present
Yocom Kent et al. (2015)	4	PP	A	F, Th+F	Present
Zhang et al. (2016)	1	PP	B	T	Absent

[a] Carbon Pools: A = Aboveground; B = Belowground; T = Total
[b] Interventions: Th = Thinning; F = Prescribed Fire; Th+F = Thinning & Fire