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Variation in tree mortality and regeneration affect forest carbon recovery following fuel treatments and wildfire

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VARIATION IN TREE MORTALITY AND REGENERATION AFFECT FOREST CARBON RECOVERY FOLLOWING FUEL TREATMENTS AND WILDFIRE

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Background Forest fuel treatments such as thinning and burning have been proposed as tools to stabilize carbon stocks in fire-prone forests in the Western U.S. Although treatments immediately reduce forest carbon storage, losses may be paid back over the long-term if treatment sufficiently reduces future wildfire severity. Less severe wildfire produces fewer direct and indirect carbon emissions, and severely burned stands may be more susceptible to deforestation. Although fire severity and post-fire tree regeneration have been indicated as important influences on long-term carbon dynamics, it remains unclear how natural variability in these processes might affect the ability of fuel treatments to protect forest carbon resources. We surveyed a wildfire where fuel treatments were put in place before fire and estimated the short-term impact of treatment and wildfire on aboveground carbon stocks at our study site. We then used a common vegetation growth simulator in conjunction with sensitivity analysis techniques to assess how timescales of carbon recovery after fire are sensitive to variation in rates of fire-related tree mortality, and post-fire tree regeneration.

Results We found that fuel reduction treatments were successful at ameliorating fire severity at our study site by removing an estimated 36% of aboveground biomass. Treated and untreated stands stored similar amounts of carbon three years after wildfire, but differences in fire severity were such that untreated stands maintained only 7% of aboveground carbon as live trees, versus 51% in treated stands. Over the long-term, our simulations suggest that treated stands in our study area will recover baseline carbon storage 10-35 years more quickly than untreated stands. Our sensitivity analysis found that rates of fire-related tree mortality strongly influence estimates of post-fire carbon recovery. Rates of regeneration were less influential on recovery timing, except when fire severity was high.

Conclusions Our ability to understand how anthropogenic and natural disturbances affect forest carbon resources hinges on our ability to adequately represent processes known to be important to long-term forest carbon dynamics. To the extent that fuel treatments are able to ameliorate tree mortality rates or prevent deforestation resulting from wildfire, treatments may be a viable strategy to stabilize existing forest carbon stocks.

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1 Introduction

As society attempts to manage forests as sinks to offset anthropogenic increases in atmospheric carbon, there has been an effort to understand how human and natural disturbances impact forest carbon stocks at time scales important to carbon sequestration. Unlike many disturbances that are completely outside or completely within the control of humans (i.e., drought or land use change), wildfires are responsive to management decisions such as fire suppression or fuels manipulation. Nonetheless, many of the factors that influence fire regimes (ignitions, climate or weather) and the corresponding impacts on forest carbon resources remain beyond our control or prediction. There are some indications that management actions that reduce wildfire severity may promote the size and/or stability of forest carbon stocks in wildfire-prone forests (Schulze et al. 2000, Hurteau et al. 2008, Hurteau and Brooks 2011). Forest fuel reduction treatments such as thinning and burning have been proposed as tools to reduce carbon losses from wildfire by proxy of reducing future wildfire severity (Wiedenmeyer and Hurteau 2010, North and Hurteau 2011). However, these treatments also reduce forest biomass and therefore forest carbon storage (Boerner 2008, Stephens et al. 2009). This sets up an inherent tension between carbon storage and fuel treatments that has been the focus of recent debate (Mitchell et al. 2009, Hurteau and North 2009, Reinhardt and Holsinger 2010, Wiedinmyer and Hurteau 2010 and replies, Hurteau and Brooks 2011). Although we have a great deal of observational and experimental information about the short-term impacts of wildfire and fuel management on forest carbon budgets (Mission et al. 2005, Campbell et al. 2007, Boerner et al. 2008, Campbell et al. 2009, Stephens et al. 2009, Meigs et al. 2009, Dore et al. 2010), long-term studies rely heavily upon simulation results and are less conclusive (Hurteau and North 2009, Mitchell et al. 2009, Reinhardt and Holsinger 2010, Sorenson et al. 2011). It remains unclear how natural variation in wildfire severity or post-fire vegetation recovery might affect the ability of fuel treatments to protect forest carbon (McKinley et al. 2011).

Forests in the United States are thought to be an overall carbon sink, absorbing approximately 10% of annual US emissions (Woodbury et al. 2007), but forest carbon stocks are susceptible to loss through human and natural disturbances. Wildfires emitted the equivalent of 4-6% of annual anthropogenic emissions in the United States between 2001 to 2007 (Wiedinmyer and Neff 2007). Severely burned stands may remain a net carbon source for years to decades following wildfire and may require a century to replace pre-disturbance carbon storage (Law et al. 2003, Meigs et al. 2009, Dore et al. 2010, Potter et al. 2011). Recent increases in the frequency, size, and severity of wildfires in parts of Western North America (Westerling et al. 2006; Miller et al. 2009, 2011) have prompted concern over the future of carbon storage in fire prone forests.

Fuel reduction treatments are widely used management tools that allow us to modify wildfire behavior and reduce the potential for stand replacing fire (Agee and Skinner 2005). Although there have been cases where fuel treatments do not reduce the severity of fire due to extreme fire weather, insufficient removal of fuels, small treatment units, or vegetation growth since treatment (Weatherspoon and Skinner 1995, Martinson et al. 2003, Safford et al. 2009, Hines et al. 2011), fuel treatments have been shown to reduce fire severity and rates of tree mortality when management sufficiently reduces surface, ladder, and canopy fuels (Martinson and Omi 2008, Safford et al. 2009). In terms of carbon, North and Hurteau (2011) observed large reductions in fire severity and wildfire emissions in stands where 18-33% of aboveground carbon was removed during treatments completed 5 years before wildfire. This range of biomass removal rates is similar to those reported in studies where fuel treatments successfully reduced simulated wildfire effects (Finkral and Evans 2008, North et al. 2009, Stephens et al. 2009). Treated stands are thought to maintain similar or smaller total forest carbon stocks than do untreated stands immediately after wildfire, because fuel treatments often remove more carbon than is saved through reductions in pyrogenic emissions, limiting the perceived carbon benefit of fuel treatments in the short-term (Reinhardt and Holsinger 2010, North and Hurteau 2011). However, successfully treated stands maintain a higher proportion of carbon as live vegetation following fire, suggesting that the potential carbon benefit of fuel treatments may be realized on a longer time scale, as fire-killed trees in severely burned stands continue to emit carbon and surviving vegetation continues to sequester carbon (North and Hurteau 2011, Hurteau and Brooks 2011, Dore et al. 2010, Meigs et al. 2009).

Over longer time periods, forest carbon storage is controlled by the balance between carbon accumulation through photosynthesis, carbon loss through decay, and offsite removal or non-biological carbon emissions including pyrogenic emissions (Net Ecosystem Production, NEP, Lovett et al. 2006). Fuel treatments will only be able to promote additional carbon storage if they cause NEP to be more positive over a long time period as compared to untreated stands. Over a fire return interval, NEP will be largely governed by direct carbon losses from wildfire or fuel treatments, indirect emissions as fire-killed trees decay, and by the growth of surviving and regenerating vegetation (Kashian et al., 2006, Hurteau and Brooks, 2011). There is clear evidence that fuel treatments are able to reduce overall carbon losses from wildfire if they are able to reduce wildfire emissions and tree mortality rates (Meigs et al. 2009, Dore et al. 2010, North and Hurteau 2011). Unfortunately, both emissions and tree mortality are difficult to predict and highly uncertain on multiple spatial and temporal scales. Fire simulators such as FVS-FFE use well-established empirical models to predict first order fire effects (Hood et al. 2007). However, a number of stochastic factors (such as fire weather, fuel conditions or ignition timing) make prediction of specific fire effects difficult (Finney 2005). Fuel treatments may fail to reduce fire severity and treatment efficacy is known to decline with time (Hudak et al. 2011). Like wildfire effects, post-wildfire regeneration may be difficult to predict. Previous research has shown that post-fire regeneration patterns may be highly temporally and spatially variable along gradients of disturbance severity, species characteristics, climate, microsite conditions, and competitive factors (Larson and Franklin 2005, North et al. 2005, Savage and Mast 2005, Grey et al. 2008, Zald et al. 2008, Meigs et al. 2009). Although wildfires may promote the regeneration of fire-adapted species, severe wildfires may cause temporary or permanent shifts in the structure or composition of forest communities (Rodrigo et al. 2004, Nagel and Taylor 2005, Savage and Mast 2005, Franklin 2006). Predictions of long-term forest carbon storage after wildfire which do not take into account uncertainties in important ecosystem processes that affect rates of carbon accumulation (such as mortality or regeneration) may contribute to the controversy over the carbon costs and benefits of fuel treatments without producing results that are transferrable to management (McKinley et al. 2011, North and Hurteau 2011).

Recent studies have used vegetation growth and fire simulation platforms to investigate the long-term impacts of fuel treatment and wildfire upon forest carbon stocks in fire prone forests (Table 1; Hurteau and North 2009, Mitchell et al. 2009, Reinhardt and Holsinger 2010, Diggins et al. 2010, Sorenson et al. 2011). All five studies reviewed simulated a short-term reduction in stand carbon (range 25% to 43%) due to fuel treatment, in agreement with observational studies of fuel treatments (Stephens et al. 2009). Three of five studies reported that treated stands showed reduced emissions or tree mortality during simulated wildfire events. None of the studies reported that treated stands would store more total C after wildfire, in agreement with observational experiments (North and Hurteau 2011). Although these studies generally agree about the likely short-term impacts of fuel treatment and wildfire on stand carbon, their long-term predictions are more varied. Over long time scales (100 years), only two studies reported that fuel treatments benefited carbon storage with benefits limited to forest ecosystems adapted to frequent fire where fire suppression has resulted in uncharacteristically dense forests (Hurteau and North 2009, Mitchell et al. 2009). However, it is difficult to discern whether these simulation studies provide reliable predictions of the long-term effects of disturbance on stand carbon storage, as they fail to address how uncertainty in fire effects or post-fire vegetation recovery impacts their conclusions regarding long-term C budgets. To date, investigators have not reported modeled rates of tree regeneration following wildfire (Table 1), even though regeneration density is known to play an important role in post-wildfire carbon recovery (Kashian et al. 2006). Similarly, many studies model mortality during wildfire without examining how variation in fire weather, fuel treatment / wildfire timing or other factors that influence fire severity might affect their results. As such, it remains unclear how natural variation in fire-related mortality and post-fire vegetation recovery may affect the role of fuel treatments in protecting forest carbon resources over the long-term.

In this study, we use information collected from fuel treated and untreated stands that burned in a natural mixed severity wildfire, along with a commonly used vegetation simulator to address the following questions: 1) What was the impact of fuel treatments and wildfire on carbon storage in treated and untreated stands in our study area?; 2) How long will treated and untreated stands take to recover pre-disturbance carbon storage? and more generally 3) How is forest carbon recovery after wildfire sensitive to variation in fire-related tree mortality and rates of post-fire tree regeneration? By answering these questions, we hope to provide context to how natural variability in wildfire severity and post-wildfire recovery might influence the ability of fuel treatments to protect forest carbon storage.

2 Methods

General overview

We collected vegetation, mortality, and regeneration data in treated ("Treated Burned"; TB) and untreated ("Not Treated Burned"; NTB) forest stands which burned in a recent mixed severity wildfire. We used these data in conjunction with the Western Sierra variant of the Forest Vegetation Simulator (FVS, Dixon 2002) to estimate forest carbon stocks and to simulate forest growth processes. FVS is an individual-tree, distance independent, growth and yield model that is widely used by academic and agency researchers investigating how management, disturbance, and climate change affect forest carbon storage (Hurteau and North 2008, Nunery and Keeton 2010, Ager et al. 2010). We estimated the size of five aboveground carbon pools in TB and NTB stands (live trees, dead trees, coarse woody debris, fine woody debris, litter and duff) in our study area before and after thinning and wildfire, in order to characterize the pre- and post-disturbance aboveground carbon storage, and fluxes due to disturbance. We then used FVS to simulate vegetation growth after fire to compare timescales of post-fire carbon recovery between TB and NTB stands, and assess how differences between modeled and observed estimates of tree mortality influenced recovery timing. Finally, we used observations of mortality and regeneration rates acquired over three years at our study site to bound the range of potential fire effects and regeneration trajectories in our study area to use as inputs to a sensitivity analysis. For our sensitivity analysis, we assessed how the timing of carbon recovery after fire is sensitive to variation in rates of fire-related tree mortality, and post-fire regeneration. We used two meaningful baselines (pre- and post-fuel treatment carbon stocks) to estimate recovery timing.

2.1 Study Site Description

The Angora fire is located within the Lake Tahoe Basin (LTB), in the Sierra Nevada of California and Nevada (Figure 1). Elevations in the basin range from 1800 m to 3315 m at Freel Peak. The climate is Mediterranean, with warm dry summers and cold wet winters. At the South Lake Tahoe, CA airport (1900 m elevation, 3 km E of the Angora Fire), the January mean minimum temperature is -10.4 ºC, July mean maximum is 23.5 ºC. Precipitation averages 784 mm per year, with 86% of precipitation falling as snow between November and April (WRCC, 2011).

Forest Fires in the Lake Tahoe Basin

Pre-settlement fire return intervals in the Tahoe Basin were 5-30 years in *Pinus jeffreyi* dominated forests and 20-45 years in upper montane forests dominated by *Abies magnifica* (Stephens 2001, Taylor 2004, Nagel and Taylor 2005, Beaty and Taylor 2008). Between 1873 and 1900, most LTB forests (including our study site) were heavily logged or clearcut and extensively grazed until the 1930s (Leiburg 1902, Taylor 2004). Over the last century, active fire exclusion in the LTB has nearly eliminated fire as a natural process. The history of logging and fire exclusion has resulted in increases in tree density, canopy cover, and surface fuels in many areas (Murphy and Knopp 2000, Taylor 2004). Before the Angora fire, only three sizable natural wildfires have occurred in the LTB in the last 100 years, largely due to effective fire suppression (Safford et al. 2009).

The Angora Fire

On June 24, 2007 the Angora wildfire was ignited from an illegal campfire and burned 1106 forested hectares (1243 total ha) over eight days. The Angora fire burned early in the fire season, under record dry conditions for that date (Murphy et al. 2007). More than half of the burn area experienced >75% tree mortality according to remotely sensed estimates of burn severity (Safford et al. 2009). About two-thirds of the fire burned in the first day, after which winds moderated and shifted to the north.

Elevations in the Angora fire range from 1900 m on the northern boundary to 2310 m on the SW boundary. Soils are generally coarse textured and well drained. Geologic substrates are primarily granitic, with some metamorphic formations on upper slopes. Slopes range from 0-5% along the Angora creek drainage to >40% along the western and southwestern borders of the fire.

Vegetation is primarily conifer forest with Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*) dominating lower slopes, and red fir (*Abies magnifica*) primarily occurring on slopes above 2100 m. Incense cedar (*Calocedrus decurrens*), sugar pine (*P. lambertiana*), lodgepole pine (*P. contorta var. murrayana*) and Quaking aspen (*Populus tremuloides*) are also present in minor amounts, with the latter two species concentrated along drainages. Montane chaparral is found on east-facing slopes along the south and western boundaries of the fire and in scattered patches elsewhere, dominated by *Arctostaphylos patula, Quercus vaccinifolia, Chrysolepis sempervirens* and species of *Ceanothus*. The last recorded fire in the Angora area was a wildfire in 1882 (Nagel and Taylor 2005), which overlapped with areas of montane chaparral and white fir forest burned by the Angora fire.

Fuel treatments in the Angora Fire Area

Approximately 182 ha (16%) of the burn area had been treated for fuels between 1996-2006 (Figure 2). Treatments generally consisted of a pre-commercial hand thin, a commercial thin and 'salvage' of standing dead material, followed by hand piling and burning. Mechanical thinning prescriptions called for a residual basal area of $36.7 m^2 ha^{-1}$ for trees >25.4 cm DBH in mechanically thinned stands, and snags less than 76.2 cm diameter were cut. Hand thinning left all trees greater than 35.6 cm DBH, and removed smaller trees to achieve an average bole spacing of 6.1 m. Crews were instructed to hand pile all thinning residues, as well as undecayed coarse woody debris (for a complete description of treatment prescriptions see Murphy et al. 2007 or Safford et al. 2009). Pre-fire fuel loadings in the Angora fire were estimated at 11 tons biomass ha^{-1} in treated stands and 57.9 tons ha^{-1} in neighboring untreated forest (Safford et al. 2009).

2.2 Sampling and Measurements

2.2.1 Plot selection Procedures

For three subsequent summers after the Angora fire, we established and surveyed eighty-six permanent vegetation plots in and around the wildfire on a 400-m grid using USFS Region 5 Common Stand Examination (CSE) protocols detailed below (USDA 2008, Figure 2). We use a subset of these plots in our analysis, selecting only plots that burned within the first twenty-four hours of fire ignition. Sixteen plots were located in stands that had been treated before wildfire (TB stand). We excluded three of sixteen TB plots from analysis because they were located in a treatment unit where piles had not been burned before the fire and where logging occurred after the fire, for a total of 13 TB plots. Twenty-nine plots were located in stands that were not treated before burning in the wildfire (NTB stand) and were within 800 m of treated stands. Three NTB plots located in densely stocked riparian areas dominated by *P. contorta* and *P. tremuloides* were excluded from analysis for a total of 26 NTB plots. Treated and untreated stands were identified using a GIS layer of treatment history obtained from Lake Tahoe Basin Management Unit staff and field verifying the maps with observations of recently cut stumps (as per Murphy et al. 2007 and Safford et al. 2009)

We also surveyed nine treated and nine untreated plots just outside the wildfire using CSE protocols. We used fuels information from plots outside the fire to estimate fuel loading in treated and untreated stands before wildfire. Most unburned plots were adjacent to the fire, but we were forced to sample five plots (3 TB, 2 NTB plots) outside of the immediate vicinity of the fire because of the lack of comparable forest area. We used previously established USFS plots when possible, and identified treatment history using USFS treatment records and field verification. Unburned plots were all located within a few kilometers of the fire, and selected based on their age, density, and species composition. Given the clearcut logging that occurred throughout the LTB in the 1890's, forest stands in this area have a similar age, species composition and forest structure, so estimates of fuel loading from outside the fire should be representative of pre-fire fuel conditions in treated and untreated stands.

Two hundred "regeneration" plots were also established on a 200-m grid across the fire. Each CSE plot had a co-located regeneration plot at its center. Regeneration plots that were logged after fire were removed from the analysis, leaving 37 and 71 plots located in treated and untreated stands, respectively.

2.2.2 Field Protocol

Common Stand Exam plots

CSE plots were circular, with an area of 809.37 m^2 (16.06 m radius, equal to 1/5 acre). In 2008 (one year after fire) we tagged live trees above a breakpoint of 12.7 cm DBH, and snags above 25.4 cm DBH on each CSE plot. For each above-breakpoint tree and snag in 2008, we recorded the species, diameter, pre- and post-fire mortality status and post-fire live crown ratio. A subset of tree heights (first five mature trees on each plot) was recorded. Above-breakpoint trees and snags in the burn area were revisited in 2009 and 2010, when we recorded further mortality, insect/disease damage, stem breakage, or tree cutting. Trees below the breakpoint were counted and tallied by species, mortality status, and diameter (2.54 to 12.7 cm and 12.7 to 25.4 cm DBH). Because we were unable to determine whether dead small trees had been alive or dead before the fire, we assumed they were alive. Although this could upwardly bias our estimates of pre-fire live tree carbon, it will also downwardly bias estimates of pre-fire snag carbon. We tallied stumps in 12.7 cm size classes on each plot to assess thinning impacts on tree carbon.

Surface woody fuels were surveyed on CSE plots using standard planar intercept protocol (Brown 1974, Waddell 2002). On each plot visit, we surveyed four 15.24 m fuels transects radiating from plot center in four cardinal directions. On all four transects, we counted fuels <0.64 cm and 0.64-2.54 cm diameter along a total of 12.19 m and fuels 2.54 – 7.62 cm diameter along 30.48 m, beginning at the distal end of the transect. We recorded the diameter and decay class of logs >7.62 cm diameter for any piece >1 m in length that intersected any transect. We recorded additional log measurements in 2010, including small and large end log diameters and log length (Waddell 2002). We also took two litter and duff depth measurements on each fuels transect, for a total of eight depth measurements per plot.

Regeneration plots

We surveyed regeneration plots in the summer of 2008, and re-visited these plots in 2009 and 2010. At each 60 m^2 circular plot we tallied tree seedlings by species and age, separately counting planted, natural, and pre-fire regeneration. Seedlings were identified to species using Franklin, 1961.

At each regeneration and CSE plot, we assigned a plot-wide categorical severity class (1-5) based on guidelines-related to fire effects on trees and vegetation. A severity rating of 5 denotes sustained crown fire across the plot, a rating of 4 indicates high mortality but no sustained crown fire, a rating of 1 indicates a ground fire that incompletely consumed surface vegetation and killed few trees, while a rating of 2 or 3 represents intermediate levels of fire severity and mortality (adapted from USDI National Park Service 2003).

2.3 Short-term impact of treatment and wildfire on C pools

We estimated the carbon density (Mg C ha-1) of five aboveground biomass pools (live trees, snags, coarse woody debris, fine woody debris, litter/duff) at five time steps (pre-treatment, pre-wildfire, 2008, 2009, 2010) in treated and untreated stands in our study area, using published allometric equations implemented in FVS-WS (Table 2). To estimate pre-thinning and pre-fire C storage, we used indirect methods because we did not survey plots before wildfire. Specifically, we used fuels data from unburned plots to estimate pre-disturbance C stocks, and stump surveys and observations of tree mortality during fire to reconstruct pre-thinning and pre-wildfire tree lists. We directly estimated the density of C pools after fire, using observations from CSE plots. We used a two-sided Wilcoxon rank sum test to test for differences in total aboveground C and component C between TB and NTB stands at each time step, using the statistical analysis software R (version 2.10.1). See Appendix A for further detail on biomass estimates.

2.4 Long-term impact of treatment and wildfire on C pools

A secondary objective of this study was to assess how fuel treatments and wildfire impacted long-term carbon resources in treated and untreated stands at our study site. We used observations of tree mortality, tree regeneration, and fuel loading made at CSE plots in 2010 in treated and untreated stands to initialize FVS, grow the stands forward, and calculate the years elapsed before the stands recovered baseline carbon stocks. We then assessed how using a fire simulator to predict tree mortality might influence our results. To do so, we repeated the same steps as above, but used a model (FVS-FFE) instead of observational data to predict tree mortality rates during wildfire. We parameterized the fire model using reconstructions of pre-fire stand conditions and fuel moisture and fire weather conditions recorded during the day of the fire (Appendix 1, Murphy et al. 2007).

The same regeneration rates were applied to each model run (observed and modeled mortality), using observations made at regeneration plots co-located with the 13 treated and 26 untreated plots used in analysis. Naturally occurring regeneration rates in the 13 treated and 26 untreated CSE plots used in these simulations averaged 479.2 and 148.8 seedlings ha-1, respectively. If no regeneration was present in 2010, we added 165 white fir seedlings ha-1 twenty years into the simulation to avoid simulating deforestation.

2.5 Sensitivity Analysis

We assessed how variation in two key ecosystem processes (tree mortality and regeneration) influenced years until carbon recovery after wildfire in treated and untreated stands. We used pre-treatment carbon density in untreated stands as our primary reference point for estimating years until recovery, as it represents baseline forest conditions before carbon losses due to fuel treatment or wildfire. However, we recognize that post-treatment conditions may be a more appropriate target for management (*sensu* Hurteau and Brooks 2011), and explored how the use of an alternate reference point (post-treatment carbon density) affects our results. To accomplish our sensitivity analysis, we initialized FVS with reconstructions of pre-fire (post-treatment) stand conditions in TB and NTB stands. We then simulated five levels of fire-related mortality and five levels of post-fire regeneration, using information collected in our study area to bound these variables as described below. We used FVS to simulate mortality, regeneration, decay, and growth over a 150 year time period, and calculated the time required to recover pre-treatment (and post-treatment) carbon stocks at each level of mortality and regeneration, for treated and untreated stands. FVS reports stand level metrics on 10 year time steps, so we used linear interpolation to estimate a specific year of recovery.

2.5.1 Mortality

We used observations of mortality rates from the 39 CSE plots in our study area to define five mortality scenarios for sensitivity analysis. We pooled estimates of tree mortality rates by diameter class for all the CSE plots in each of four categorical fire severity classes to create four mortality scenarios (Table 3). We created a central fifth mortality scenario by averaging mortality rates from severity categories 2 and 3, in order to model a full range of mortality rates (Table 3). Each of the five mortality scenarios defines a different mortality rate for four tree diameter classes (0-25.4 cm, 25.5 cm to 50.8 cm, 50.9 to 76.2 cm, and 76.3+ cm), based on data from our study site. Overall mortality rates range from 30% in the least severe scenario to 100% mortality in the most severe. We recognize that more intense fires are associated not only with higher tree mortality, but also produce more emissions from surface carbon pools (Meigs et al. 2009, Campbell et al. 2007). Each of five mortality scenarios had an associated set of combustion factors that were applied to pre-fire surface carbon pools (fine woody debris, coarse woody debris, litter and duff) to differentiate between the impact of less and more severe wildfire on stand carbon storage (see Appendix A for rates). We used previous research as the basis for setting our combustion co-efficients (Campbell et al. 2007).

2.5.2 Regeneration

We chose to represent variation in regeneration using a simple model, where we varied post-fire regeneration at one of five densities between 165 to 1400 seedlings ha^{-1}, split evenly between Jeffrey pine and white fire, and did not add additional regeneration during the simulation period. These regeneration rates were selected by varying the median seedling density of all plots containing regeneration (670 seedlings ha-1) by plus or minus 50% and 75% (Figure 4). The five regeneration rates chosen fell within the range of pre-disturbance forest densities reconstructed at our study site (197 to 1754 trees ha^{-1}, median ~800 trees ha^{-1}). We explored how allowing for additional regeneration throughout the modeling period influenced our results (Appendix A), and found that the use of more sophisticated regeneration models did little to change our general conclusions.

3 Results

3.1 Short-term impact of treatment and wildfire on C pools

Before disturbance by fuel treatments or wildfire, treated and untreated stands in the Angora burn area stored comparable amounts of aboveground carbon (183.2 and 175.89 Mg C ha-1 respectively, Wilcoxon rank sum test p value = 0.758, Table 3). In treated stands, carbon losses due to fuel treatment (tree removal and pile burning) totaled 70.48 Mg ha-1 (or 38% of aboveground C). We estimate that roughly 40% of C losses during treatment were due to tree removal (28.3 Mg C ha-1), and 60% to pile burning (values based on observations of stumps and the difference in average surface fuel loads between treated and untreated plots outside the fire [42.15 Mg C ha-1]). Before wildfire and after fuel treatments, TB stands stored significantly less aboveground carbon than NTB stands (111.85 and 175.51 Mg C ha-1, respectively, Wilcoxon rank sum test p-val = 0.0002). After wildfire, treated and untreated stands stored similar amounts of total aboveground carbon (89.27 and 101.08 Mg C ha-1, respectively, rank sum test p-val > 0.5). Pre- and post-wildfire estimates of aboveground C storage were 22.58 and 74.43 Mg C ha-1 lower in treated and untreated stands respectively, suggesting overall pyrogenic emissions of 20% to 42%.

Although total post-fire C storage did not differ between treatments, untreated stands stored significantly more carbon in non-living pools (snags and CWD). Carbon contained by dead trees and coarse woody debris represents 84% of all aboveground C in untreated stands in 2010, and 28% in treated stands. Likewise, treated stands maintained more live tree carbon after fire. Treated stands retained 55% of aboveground C as live tree C in 2010, while untreated stands maintained 6.5% aboveground C as live trees in 2010. We observed continued tree mortality throughout the three years of our study. Mortality occurring within one year of fire (through 2008) represented 73% and 96% of all live tree C that died as a result of fire in treated and untreated stands, respectively.

From regeneration plots surveyed in treated and untreated stands (n=37 and n=71, respectively), we estimated that treated stands have lower mean seedling densities than untreated stands (794.74 vs. 2765.14 natural seedlings ha-1, Table 4) three years after fire. However, median rates of regeneration in treated stands are higher than those in untreated stands (518.93 vs. 0 seedlings ha-1), as 51% of plots in untreated stands had no natural tree regeneration three years after fire, vs. only 14% of plots in treated stands. (see Appendix B for more detailed information).

3.2 Long-term impact of treatment and wildfire on C pools

Three years after wildfire, we observed that treated stands in the Angora fire experienced 53% overall lower rates of tree mortality than untreated stands (mean 31% [sd 24%] vs. mean 84% [30%] basal area mortality, respectively, Figure 5a). Rates of mortality predicted by FVS-FFE were lower than observed rates in treated stands (predicted mean 21% [27%] vs. observed 31% BA mortality) and higher than observed rates in untreated stands (predicted 99% [2%] vs. observed 84% BA mortality, Figure 5b).

We then assessed how differences between observed and modeled tree mortality might influence time scales of recovery in stands in our study area. Using pre-treatment carbon (175 Mg C ha-1) as a baseline, treated stands recover baseline C stocks 10 years more quickly on average than untreated stands (83 vs. 93 years, respectively, Figure 6a), when simulations are parameterized by observed mortality rates. Simulations parameterized by FVS-FFE estimated mortality show treated stands will recover C stocks 34 years more quickly than untreated stands (in 58 vs. 92 years, respectively).

Using post-treatment carbon (111.85 Mg C ha-1) as a baseline, treated stands recover baseline C stocks 35 years more quickly than untreated stands (28 vs. 63 years, respectively, Figure 6b) when simulations are parameterized by observed mortality rates. Simulations parameterized by FVS-FFE estimated mortality show treated stands will recover C stocks 50 years more quickly than untreated stands (in 14 vs. 64 years, respectively).

3.3 Sensitivity analysis

At the start of FVS simulation, treated stands contained 36% less C than untreated stands (111.85 vs. 175.51 Mg C ha-1). We estimated that treated stands would recover pre-treatment carbon stocks (175 Mg C ha-1) over a range of 52 to 138 years , while untreated stands required 28 to 128 (Figure 7). Mortality rates strongly influenced the timing of carbon recovery, regardless of treatment status. Severely burned stands recovered carbon about 20 years more slowly than stands experiencing low mortality rates, when regeneration rates were high. At low rates of regeneration, mortality more strongly influenced the timing of recovery. Stands that experienced low and moderate rates of mortality required 30-60 fewer years to recover C than stands that experienced mortality rates over 80%.

Regeneration rates were not influential on the timing of recovery at low rates of mortality, but were influential at 65% and higher rates of mortality. Above this level of mortality, stands that had high regeneration rates recovered carbon 30-45 years sooner than sparsely regenerated stands (Fig. 7).

We examined how using a different baseline of 112 Mg C ha-1 (post-treatment instead of pre-treatment carbon density) affected our estimates of carbon recovery timing (Figure 8). Treated stands were estimated to recover post-treatment baseline storage in 11 to 87 years after disturbance, depending on the level of regeneration or mortality. This range of recovery times is about 40 years faster compared to using a pre-treatment reference baseline.. Regardless of our chosen baseline, recovery times respond strongly to mortality rates, and to regeneration rates when mortality is high.

4 Discussion

We used data collected in treated and untreated forest stands that burned in a natural wildfire to investigate the short- and long-term consequences of fuel treatment and wildfire on forest carbon resources. We more generally investigated how long-term carbon recovery after wildfire is sensitive to variation in wildfire-related tree mortality and post-fire tree regeneration using a sensitivity analysis. Our short-term estimates of the direct impacts of fuel treatment and wildfire from the Angora fire show that although fuel treatments may reduce carbon emissions and mortality rates resulting from wildfire, treated stands still store similar or less overall carbon than untreated stands immediately after fire. This finding corroborates evidence from previous observational (North and Hurteau 2011) and simulation studies (Hurteau and North 2009, Mitchell et al. 2009, Ager et al. 2010, Reinhardt and Holsinger 2010), which suggest that C removals during fuel treatment often exceed reductions in pyrogenic C emissions as a result of treatment. Although pyrogenic emissions may be regionally significant sources of carbon dioxide (Campbell et al., 2007), fire-related mortality of trees is the single largest carbon transformation that occurs during severe forest fires, carbon which becomes available to future release through decomposition or future fire (Auclair and Carter 1993, Campbell et al. 2007, Meigs et al. 2009). As such, reductions in fire-related tree mortality are thought to be one of the primary mechanisms by which fuel treatments are able to protect long-term forest carbon stocks, particularly when post-fire regeneration is not sufficiently dense to replace the trees killed during fire (Kashian et al. 2006, Dore et al. 2010, Hurteau and Brooks 2011).

In the Angora fire, fuel treatments were effective at reducing multiple measures of fire severity including rates of tree mortality as compared to nearby untreated stands (Safford et al., 2009). In part, the Angora treatments were successful because they were completed soon before wildfire and sufficiently reduced surface, ladder and canopy fuels by removing an estimated 36% of aboveground biomass. Although treated stands stored less carbon than untreated stands before and similar amounts immediately after wildfire, our long-term simulations suggest that treated stands will recover pre-wildfire carbon stocks 10 to 35 years more quickly than untreated stands depending on the baseline used. Although this simulation does not take into account future management or disturbance events, fuel treatments in the Angora fire seem to have been effective at protecting aboveground C stocks over a period of approximately 30-90 years, by proxy of their ability to reduce severe fire effects on vegetation.

We compared how using observed and modeled rates of tree mortality might influence our expectations of carbon recovery timing after wildfire in treated and untreated stands. Although FVS-FFE predictions of mortality were within +/- 15% of observed rates for both stands, using modeled mortality rates led to a predicted recovery time in treated stands that was 15 to 25 years longer than when using an observationally parameterized model. This finding highlights how uncertainty regarding wildfire behavior may impact our expectations regarding treatment impacts on long-term carbon dynamics. Effective fuel treatments (Agee and Skinner 2005) can ameliorate severe fire behavior, as evidenced from our study site. However, observational studies have found a high degree of variation in fuel treatment effectiveness related to variation in treatment prescription and implementation, treatment size, vegetation type, treatment/ignition timing, and fire weather conditions (see Hudak et al. 2011). Previous studies investigating the impact of fuel treatment and wildfire on long-term forest carbon storage have accounted for a number of these factors, but the prediction of specific fire effects remains difficult due to the stochastic nature of wildfire (Finney 2005).

Sensitivity analysis

Limited inferences can be made from simulations that do not incorporate a realistic range of potential wildfire effects or post-fire vegetation recovery in their modeling efforts (McKinley et al. 2011). We used sensitivity analysis techniques to investigate how variable levels of fire severity and post-fire regeneration affects post-fire carbon recovery, using observations made in our study site to bound our analysis. We found that timescales of carbon recovery after disturbance are highly sensitive to modeled rates of fire-related tree mortality and post-fire regeneration. In our analysis, mortality rates played a particularly strong role in the timing of C recovery. Time until recovery consistently increased as mortality rates increased, despite regeneration rate or treatment status. Average time scales of carbon recovery increased by 40 years when mortality increased from 30% to 65%, and another 10 years when mortality rates exceeded 90%. This suggests small variations in fire-related mortality rates may have large consequences on the prediction of stand level carbon storage over the next century.

We explicitly applied five levels of fire severity, assuming that stand structure would not affect fire severity in our sensitivity analysis. At equal levels of regeneration and mortality, treated stands always required longer to recover pre-treatment C stocks than untreated stands as treated stands were assumed to have 36% less biomass at the time of wildfire. However, if fuel treatments are able to reduce rates of wildfire-related mortality, our simulations suggest that treated stands could recover baseline C storage more quickly. For example, if a treatment reduced mortality from 88% to 49% with a regeneration density of 670 seedlings ha-1, treated stands would recover pre-treatment carbon storage 17 years more quickly than untreated stands.

We also demonstrated that assumptions regarding post-fire tree regeneration have a strong influence on long-term estimates of forest carbon recovery, particularly when stands experience a high rate of fire-related tree mortality. After severe fire, we estimated that sparsely regenerated stands may not recover pre-disturbance carbon storage for more than 100 years. After less severe fires, regeneration played a less important role, as surviving trees were responsible for most of the carbon recovery after fire. Although we used a simple model of regeneration, many previous simulation studies have used static or unreported assumptions regarding regeneration, despite empirical evidence that post-fire vegetation (or the lack thereof) plays a key role in carbon accumulation following fire (Mission et al. 2005, Meigs et al. 2009, Dore et al. 2010). Because our regeneration model only accounted for regeneration in the first year after fire, we also developed two alternate scenarios that allow for regeneration throughout the modeling period beginning 20 years after fire (see Appendix A). Using alternative regeneration models did not change our general conclusion that variation in mortality and initial post-fire regeneration densities strongly impact time scales of carbon recovery. Estimates of recovery time scales using alternative regeneration scenarios were similar to those reported, except for high mortality and low regeneration scenarios where the model estimated a 20-40 year shorter time to recovery when continuing regeneration was 162 trees ha-1 decade-1.

Assumptions and appropriate inference

We made a number of assumptions when modeling mortality and regeneration in our sensitivity analysis. We assumed that mortality rates between 30% and 100% were possible for both treated and untreated stands, and did not model the effect of stand structure / fuel treatment on fire severity in this portion of our analysis. When modeling regeneration we assumed that tree seedling densities would not co-vary with modeled mortality rates and decided not to consider the possibility of deforestation or delayed reforestation. We did not consider how non-tree vegetation might affect post-fire carbon dynamics as understory vegetation is not well modeled by FVS. We focused on the role that regeneration density plays in carbon budgets and did not assess how variation in other stand characteristics (e.g. species composition or age structure) might affect our conclusions. Although we only examined how variation in one aspect of succession (tree density) is influential on carbon recovery, few other studies have explicitly examined how variation in mortality or post-fire regeneration influence predictions of stand level carbon budgets.

Our predictions of recovery timing evaluate how variation in mortality and regeneration influence carbon recovery within one fire return interval. Although fuel treatments directly impact forest carbon resources in a predictable manner, the impact of fuel treatments on long-term carbon dynamics will be mediated by future disturbances. To the extent that fuel treatments are able to reduce mortality rates during wildfire or encourage post-fire regeneration, our findings suggest that treated stands may recover carbon lost to wildfire more quickly than untreated stands.

Our sensitivity analysis did not consider how future disturbance or management regimes might affect carbon dynamics across the time period modeled. Before Euroamerican settlement, forests in our study area supported a high frequency/low severity fire regime with fire return intervals ranging from 5-30 years with a mean return intervals of ~11 years (Stephens 2001, Beaty and Taylor 2008). Under pre-settlement fire regimes, 4 to 14 fires would have been expected to burn in the study area over the temporal course of our longest recovery scenarios. Although human fire suppression has succeeded in excluding fire from most of the Lake Tahoe Basin for a century, recent fires have been bigger and more difficult to suppress. For example, all fires >200 ha in size that occurred over the last 100 years have occurred in the last decade. Future climate and fire projections under global warming and increasing human population densities suggest that fire risk will rise significantly over the next century (e.g., Flannigan et al. 2000, Lenihan et al. 2008), and indeed current increasing trends in fire activity, area, and severity in the Sierra Nevada suggest that such changes are already underway (Miller et al. 2009). A further issue is future fuel treatment plans in the study area, which falls almost entirely within mapped Wildland-Urban Interface (WUI). Treatment effectiveness in Sierra Nevada yellow pine or mixed conifer forests decreases substantially after about 10 years (Collins et al. 2008). Forest Service strategies for long-term management often assume treatment re-entries on a rotation of at least 20-30 years. There is evidence that fuel treatments may be more effective at protecting carbon in forests adapted to frequent low-severity fires (Hurteau and North 2009, Mitchell et al. 2009), but as with wildfire, our scenarios were not able to account for the potential effects of these recurrent future biomass removals.

Because our study did not incorporate future management or disturbance regimes in our analysis, it is unclear whether fuel treatments represent an appropriate long-term strategy to protect forest carbon resources at spatial and time scales compatible with carbon sequestration. However, we have shown that tree mortality and post-disturbance regeneration rates strongly influence expectations of carbon dynamics after wildfire. Although FVS-FFE is useful to model potential effects of management and disturbance upon ecosystem attributes, it is not designed as a tool to model complex ecological processes such as vegetation succession over long time scales without considerable user input (Reinhardt et al. 2001). FVS began as a mechanistic tree growth model that has expanded over time to include a number of other routines that allow the simulation of management and disturbance. FVS does not by default report uncertainty in estimates. As such it is important for model users to examine a range of plausible disturbance regimes when examining the fate of carbon in forest stands, particularly in the face of changing disturbance regimes and an uncertain future climate (Millar et al. 2007). This type of scenario building is common in landscape simulation modeling (e.g. Scheller and Mladenoff 2007) and for modeling climate change impacts. We recognize that FVS-FFE is an important tool for examining the consequences of management and disturbance on forest attributes, and our findings highlight how model inputs can influence expected outcomes.

Implications for management

In many Western forests, fire suppression has allowed biomass to accumulate beyond what would be expected under naturally occurring fire regimes (Hurtt et al. 2002, North et al. 2009, Hurteau et al. 2011). However, the carbon stored in uncharacteristically dense forests may be at risk if stand replacing wildfire occurs, due to large emissions resulting from fire and the potential for changes in vegetation type (McKinley et al. 2011). In the debate over whether fuel treatments are an appropriate management strategy to protect forest carbon resources, a number of studies have focused upon the ability of fuel treatments to mitigate increases in atmospheric carbon, by either reducing emissions resulting from wildfire, or by storing more carbon as compared to untreated stands (Millar et al. 2007, Hurteau et al. 2008, Wiedinmyer and Hurteau 2010). However, given the unpredictable nature of wildfire and the recurrent biomass removals required to effectively reduce wildfire risk, a number of studies agree that fuel treatments may be an ineffective climate mitigation strategy unless treated biomass is used in other carbon positive activities (i.e. wood products or energy generation; Finkral and Evans 2008, North et al. 2009, Reinhardt et al. 2010, Hurteau and Brooks 2011).

Hurteau and Brooks (2011) proposed that fuel reduction treatments may be better characterized as adaptive management tools that aid in stabilizing existing forest carbon stocks under a natural disturbance regime (carbon carrying capacity, Keith et al. 2009). If we decide that maintaining a fire-resistant forest structure through fuel reduction is an appropriate strategy to promote stable (but not maximal) forest carbon storage, identifying a carbon carrying capacity appropriate for the forest in question will be an important task (North et al. 2009). We found using a post-treatment carbon baseline to define carbon recovery increased the perceived benefit of fuel treatments. When we used post-treatment C stocks (112 and 175 C ha-1 in treated and untreated stands, respectively) to define baseline conditions, we found that treated stands recovered pre-fire C more quickly even if treatments did not reduce mortality rates during wildfire. If treatments do reduce wildfire related mortality from 88% to 49%, our simulations suggest that treated stands recover baseline C five times faster than untreated stands (17 vs. 85 years). Although the treated stands may not necessarily store more carbon than untreated stands at any given point when we assume two different baselines, treated stands may tolerate a number of intermediate disturbances in the same time period that it takes an untreated stand to recover from a single severe disturbance. This finding coincides with the theoretical framework provided by Hurteau and Brooks (2011), who illustrate the difference between stable and maximal carbon stocks.

Forest management activities such as thinning, prescribed burning, logging, or replanting after fire are resource intensive. Our analysis demonstrates that reducing mortality during future wildfire events should be a key goal of fuel treatments, if carbon storage is a long-term management goal. If severe fire does occur, regeneration monitoring and tree planting will be important to ensure prompt recovery of carbon stocks. Of course, long-term carbon storage is not the only critical consideration for resource managers. Fuel treatments may result in increased growth or increased reproductive output among the remaining trees, which may enable treated forests to avoid future drought- or insect-related mortality (Sala et al. 2005, Peters and Sala 2008). There is likely a tradeoff between high rates of regeneration and future fire risk, that must be navigated with future multiple resource objectives in mind (Miller et al. 2011, in press). The species composition and age structure of post-fire regeneration may also be highly important to managers seeking to maintain fire-resistant forest communities dominated by pines. Similarly, a focus on minimizing mortality may come at the cost of fire-obligate species (Hutto 2008).

5 Conclusions

Our ability to understand how anthropogenic and natural disturbances affect forest carbon resources hinges on our ability to adequately represent processes known to be important to long-term forest carbon dynamics. In this study, we showed that assumptions regarding rates of fire-related mortality and post-fire regeneration strongly influence estimates of forest carbon recovery. To the extent that fuel treatments reduce tree mortality rates during fire, or encourage post-fire tree regeneration, fuel treatments may be a viable strategy to promote more rapid recovery of pre-existing forest carbon stocks.

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Authors	Year	Time scale	Growth Model	Simulates regeneration ?	Regeneration rate	Simulates mortality in wildfire?	Modeled Mortality Rates
Diggins et al.	2010	100 years	FVS	Yes[1]	N.R.	No[6]	N.A.
Hurteau and North	2009	100 years	FVS	Yes[2]	N.R.	Yes[7]	~ 7-40%[11]
Mitchell et al.	2009	800 or 1600 years	STAND-CARB	N.R.[3]	N.R.	Yes[8]	~10-33%, 45-99%, 60-99%[12]
Reinhardt and Holsinger	2010	100 years	FVS	Yes[4]	N.R.	Yes[9]	~ 14% to 97%
Sorensen et al.	2011	100 years	FVS	Yes[5]	$13.934 \times e^{(-0.022 * \text{Basal Area})}$	Yes[10]	N.R.

[1] Regen rate from Roccaforte et al. 2010 plus 40% (as per Fulé et al. 2004), examines impact of one or two regeneration events in 100 year period
[2] Fixed annual rate adapted from Zald et al. 2008 (personal communication)
[3] Did not describe how STANDCARB treats regeneration
[4] Uses FVS Regeneration Establishment model defaults for ID/MT (Dixon 2002)
[5] Background rate as function of basal area. Rate from Bailey and Covington 2002, 20 year delay after severe fire
[6] Simulates prescribed fire with FVS-FFE, not wildfire
[7] Simulates wildfire with FVS-FFE, extreme fire conditions only
[8] Simulates wildfire with STANDCARB, using historical fire regimes to set burn frequency and severity
[9] Simulates wildfire with FVS-FFE, severe fire conditions only
[10] Simulates wildfire with FVS-FFE, severe fire conditions only
[11] Percent live tree C killed by wildfire
[12] Ranges of rates are Expected[Severity] for Coastal range, West Cascades and East Cascades of Oregon, respectively.

Table 1. Review of studies modeling the impact of fuel treatment and wildfire on long-term forest carbon, focusing on assumptions regarding wildfire-related mortality and post-fire regeneration. N.R. = not reported.

			Timestep				
C Pool	**Source of Biomass equation**	**Biomass to C factor**	**Pre-Treatment**	**Pre-Wildfire**	**2008**	**2009**	**2010**
Live trees	FVS-WS default	0.5	Prefire live treelist plus stumps	Prefire live treelist	As observed 2008	As observed 2009	As observed 2010
Dead Trees	FVS-WS default	0.5	Prefire snag list	Prefire snag list	“	“	“
Wood > 7.62 cm	Waddell et al. 2002	0.5	Surface C pools: Average from untreated stands outside fire	Surface C: pools Average from untreated **or** treated stands outside fire	“	“	“
Wood < 7.62 cm	Brown 1974, and van Wagendonk et al., 1998	0.5			“	“	“
Litter and duff	van Wagendonk et al., 1996	0.37			“	“	“

Table 2. Methods used to estimate carbon density for five aboveground pools (live trees, dead trees, large woody debris, small woody debris, and litter and duff) at five time steps on 13 treated and 26 untreated Common Stand Exam plots in the Angora fire. Live and dead tree biomass was estimated using default species specific equations in the Forest Vegetation Simulator Western Sierra variant (FVS-WS, Stage 2002).

		Carbon density (Mg C ha^{-1})			
Time Step	**Pool**	**TB stand (n=13)**	**NTB stand (n=26)**	**p value**	**Significance**
Pre-treatment	Live Tree C	108.20	96.43	0.471	
	Snag C	3.06	8.39	0.028	**
	FWD C†	3.68	3.68	n.a.	n.a.
	CWD C†	33.87	33.87	n.a.	n.a.
	Floor C†	33.52	33.52	n.a.	n.a.
	Aboveground C	182.33	175.89	0.758	
Pre-fire	Live Tree C	79.89	96.05	0.489	
	Snag C	3.06	8.39	0.028	**
	FWD C‡	2.22	3.68	0.077	*
	CWD C‡	3.85	33.87	0.019	**
	Floor C‡	22.82	33.52	0.258	
	Aboveground C	111.85	175.51	0.000	***
2008	Live Tree C	57.94	10.82	0.000	***
	Snag C	15.34	70.99	0.000	***
	FWD C	1.20	0.61	0.087	*
	CWD C	2.01	10.62	0.010	**
	Floor C	12.78	8.03	0.003	***
	Aboveground C	89.27	101.08	0.691	
2009	Live Tree C	53.27	7.66	0.000	***
	Snag C	18.51	73.65	0.000	***
	FWD C	1.66	1.11	0.159	
	CWD C	3.15	11.12	0.025	**
	Floor C	13.02	8.53	0.038	**
	Aboveground C	89.61	102.06	0.607	
2010	Live Tree C	49.59	6.93	0.000	***
	Snag C	20.33	74.28	0.000	***
	FWD C	1.81	2.16	0.368	
	CWD C	4.97	14.81	0.003	***
	Floor C	13.42	7.37	0.009	***
	Aboveground C	90.11	105.55	0.586	

Table 3. Estimates of carbon density for five aboveground C pools in treated (TB) and untreated (NTB) stands before disturbance by treatment and wildfire, and for three years after wildfire. We estimated differences in component and total carbon pools between treatments at each time step using a Wilcoxon rank sum test. †: Pre-treatment carbon densities of surface fuels are assumed to be the same in TB and NTB plots ‡: Carbon densities of surface fuels before fire were estimated as the mean from 9 treated and 9 untreated plots outside the wildfire.

Estimate	Statistic	Treated Stands (n=37)	Untreated Stands (n=71)
Total Natural Seedlings ha-1	Mean	794.74	2765.14
	Sd	893.66	13946.16
	Median	518.92	0.00
Total Planted Seedlings ha-1	Mean	65.45	151.05
	Sd	255.75	292.28
	Median	0.00	0.00

Table 4. Tree regeneration rates observed in treated and untreated stands at our study site. We report seedling density three years after wildfire (2010) without distinguishing between species, or year of establishment (see Appendix B for more complete regeneration information).

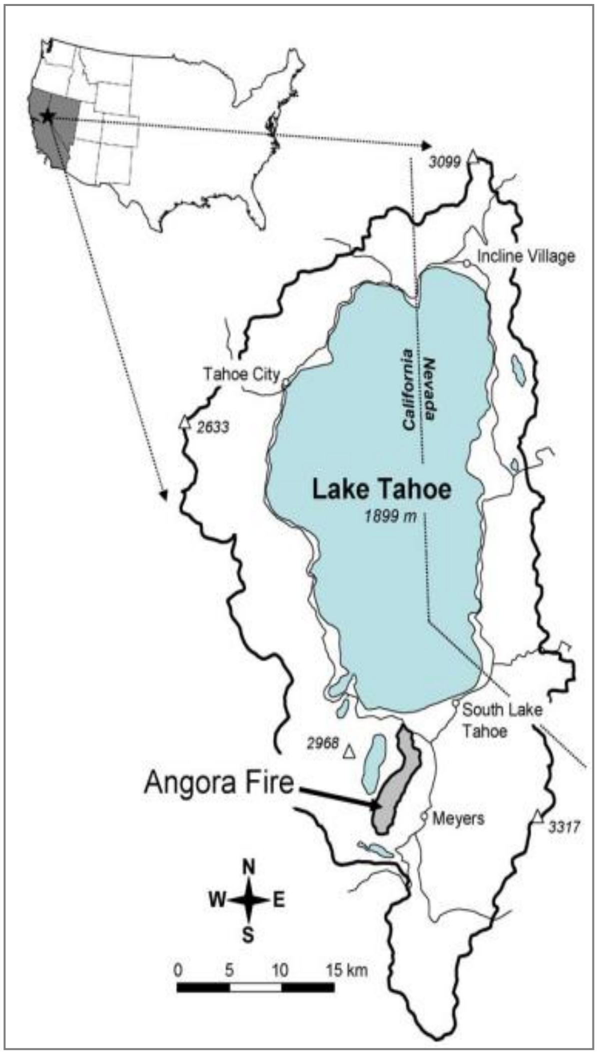


Figure 1: Location of Lake Tahoe Basin and the Angora Fire.

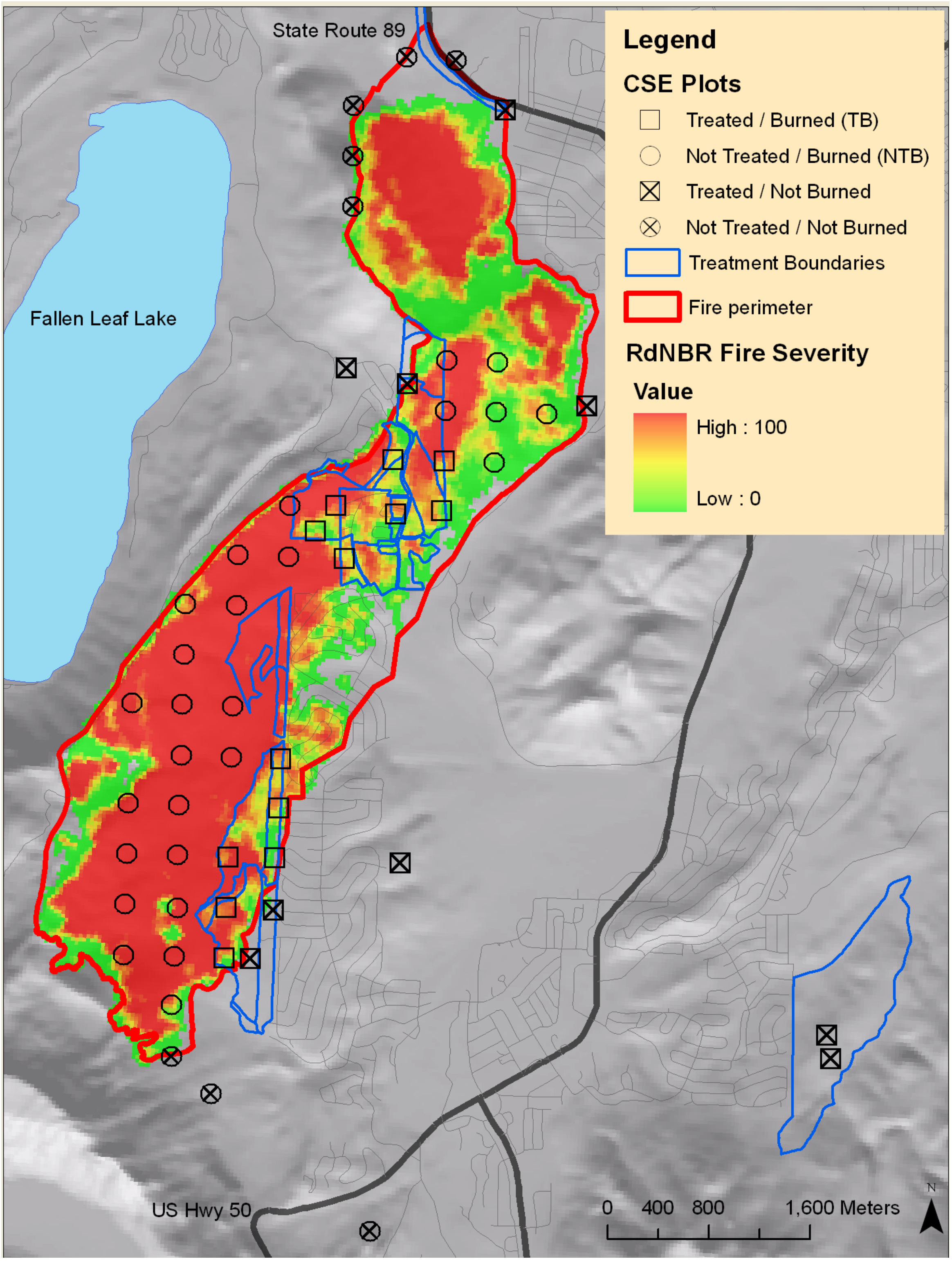


Figure 2 : Map of the Angora fire, showing a remotely sensed map of fire severity (RdNBR), overlaid with positions of Common Stand Exam (CSE) plots used in analysis. Plots located in Treated and Burned stands (TB, blue outlines) are marked with an open square (n=13), plots located in stands which were Not Treated and Burned (NTB) are marked with an open circle (n=26). Treated and untreated plots sampled outside the fire are marked with filled circles and squares, respectively (n=9 and n=9, respectively).

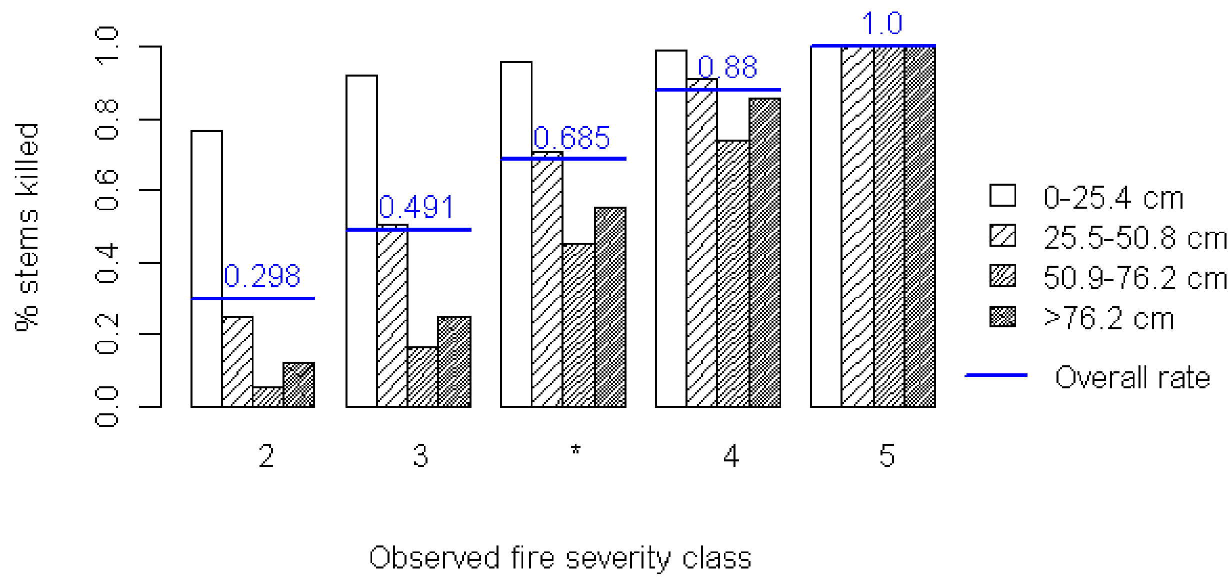


Figure 3. Mortality rates by diameter class used to define each of five mortality scenarios used in sensitivity analysis. Mortality rates in scenarios 1,2,4 and 5 were directly estimated from CSE plots in field assigned fire severity classes 2,3,4 and 5. We decided to create a central fifth mortality class (with an overall mortality rate of 68.5%) by averaging observed mortality rates in severity classes 3 and 4, to avoid a large discontinuity in our sensitivity analysis.

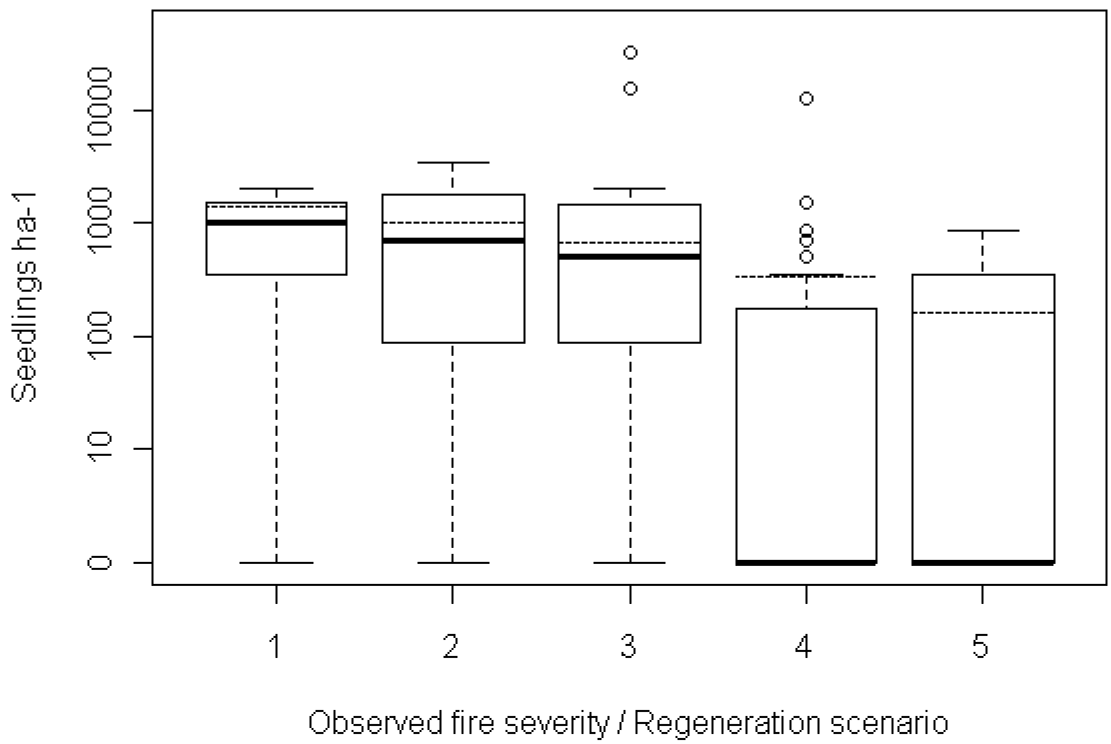


Figure 4. Density of natural conifer regeneration (log scale) observed three years after the Angora fire in five categorical fire severity classes (boxplots), overlaid with regeneration rates used in sensitivity analysis models (dashed lines). We varied regeneration rates at one of five densities (1400, 1005, 670, 335, and 165 seedlings ha-1) in our sensitivity analysis. These rates were chosen to represent a realistic range of post-wildfire forest densities, consistent with re-constructions of pre-wildfire live tree densities at our study site (197 to 1754 trees ha^{-1}).

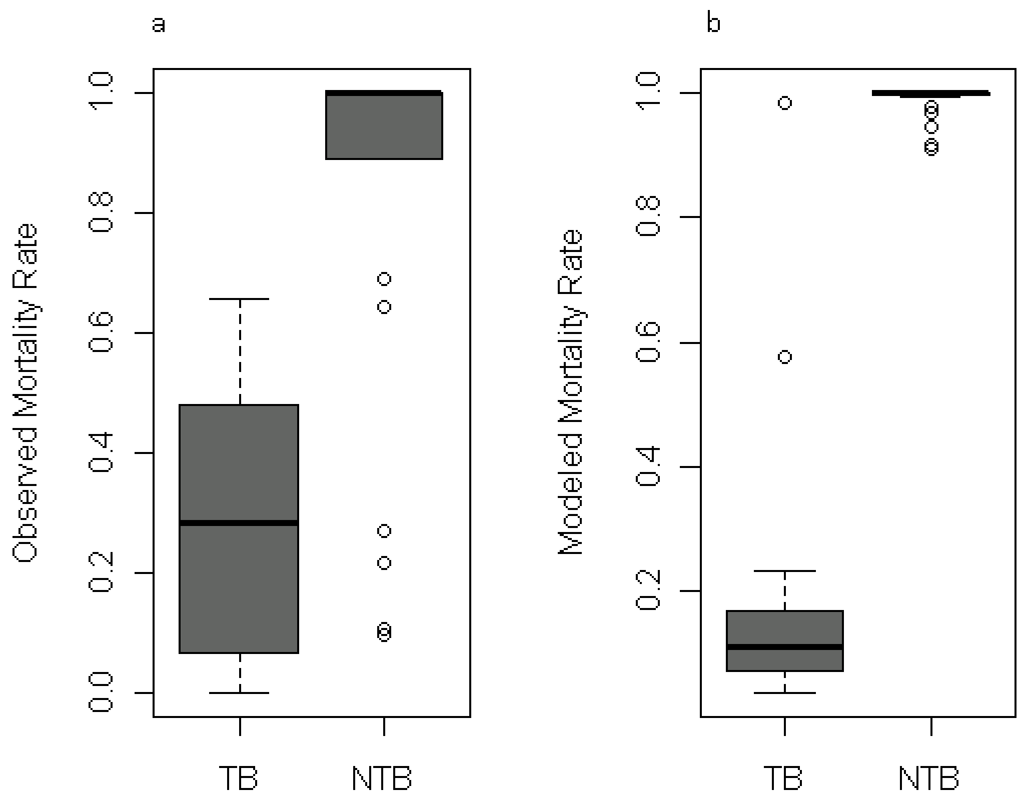


Figure 5: Rates of mortality (proportion basal area killed) estimated using (**a**) field based observations and (**b**) the Forest Vegetation Simulator Fire and Fire Effects extension to predict tree mortality (Dixon 2002, Rebain 2010), for plots located in treated (TB) and untreated (NTB) stands at our study site. See Appendix A for details regarding wildfire simulation.

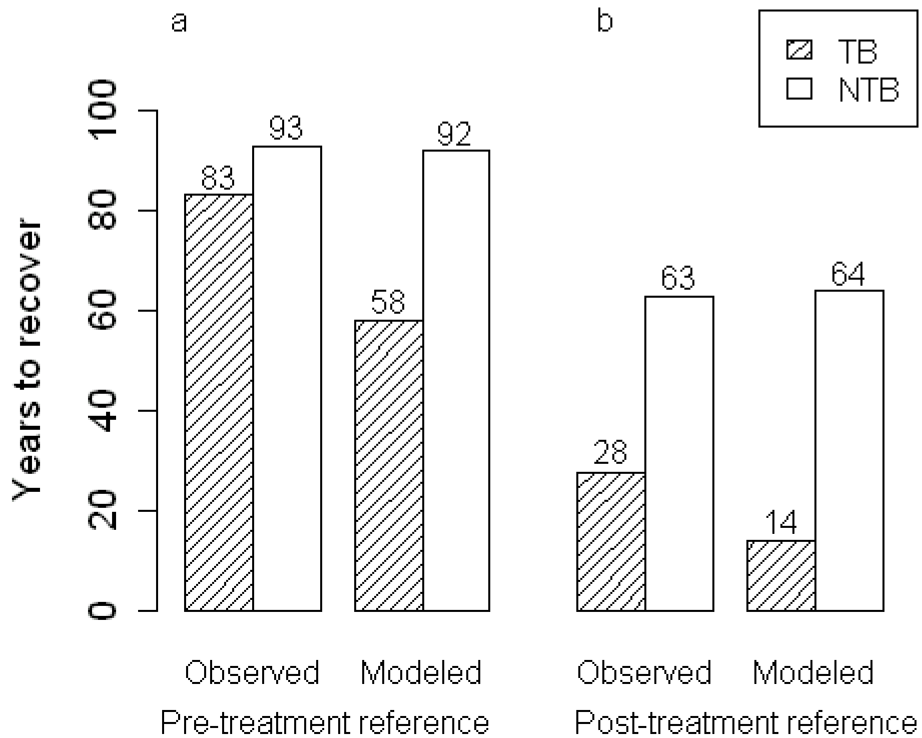


Figure 6. Time scales of carbon recovery in treated (TB, filled bars) and untreated (NTB, open bars) forest stands, using observed and modeled estimates of mortality rates to set initial conditions, using (**a**) pre-treatment carbon density (175.51 Mg C ha-1) and (**b**) post treatment carbon density (111.85 Mg C ha-1) to define the threshold of recovery. In both observational and simulation based estimates, fuel treated stands in the Angora fire are estimated to recover pre-treatment and post-treatment C stocks more quickly than stands which were not treated for fuels. Because of differences between observed and simulated mortality rates, models parameterized with simulated mortality rates suggest a greater benefit of fuel treatment on carbon recovery than using an observationally parameterized model. The choice of a reference point also strongly affects the perceived benefit of fuel treatments on carbon recovery. If post-treatment carbon density is used as a reference point, fuel treated stands are estimated to recover carbon 35 years faster than untreated stands, versus 10 years faster when using pre-treatment C density to define recovery.

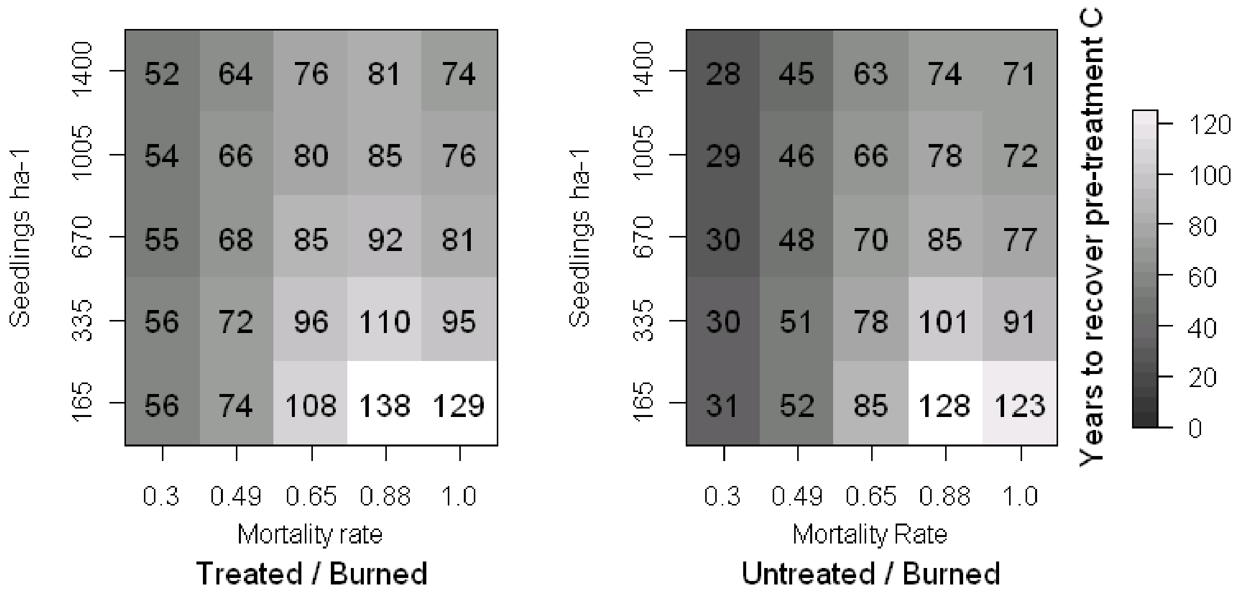


Figure 7. Sensitivity analysis results, showing number of years to recover pre-treatment baseline carbon storage (175.51 Mg C ha-1) in treated and untreated stands at each combination of five levels of mortality rates and regeneration rates.

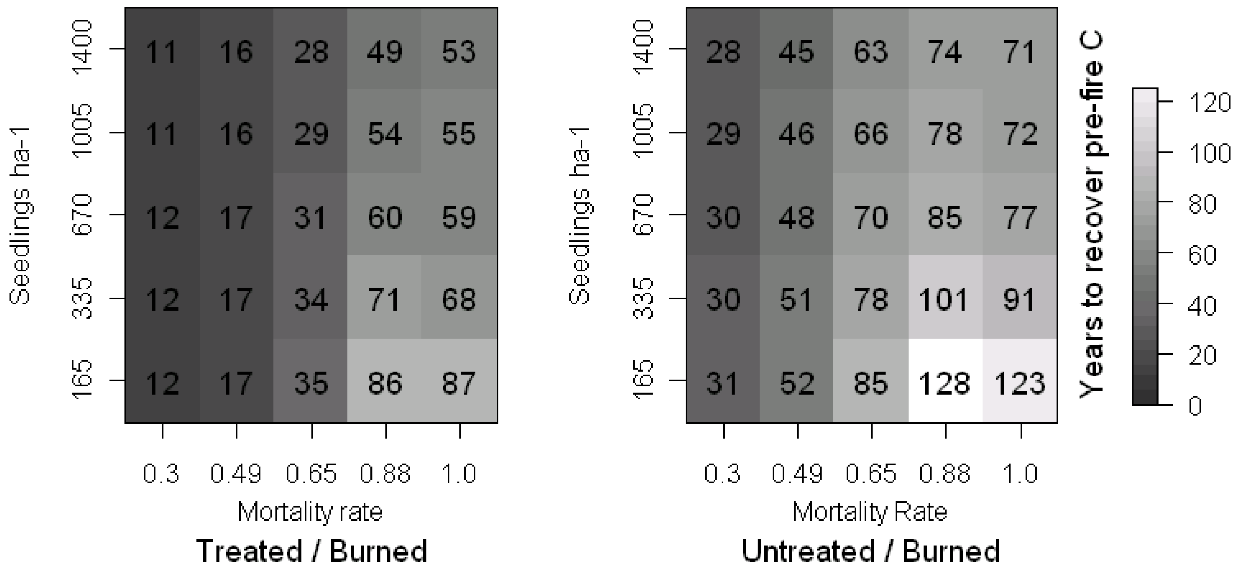


Figure 8. Sensitivity analysis results, showing number of years to recover pre-disturbance baseline carbon storage in treated and untreated stands, using post-treatment conditions as a reference point (111.81 vs. 175.51 Mg C ha-1 in treated and untreated stands, respectively) at five levels of mortality and regeneration.

Appendix A

1.0 Carbon pool estimation

We estimated the C density (measured in Mg C ha^{-1}) of the following five pools at five time steps for each of 39 plots in our study area: live trees, dead trees, fine woody debris (FWD, < 7.62 cm diameter), coarse woody debris (CWD, ≥7.62 cm diameter), and litter and duff. For the purpose of this study, the sum of these five pools is equal to aboveground C. Although understory vegetation, soil carbon and root carbon may constitute a substantial proportion of forest carbon stocks, we did not include them in our analysis for a variety of reasons. These pools are not required by many forest carbon protocols, are not well modeled in FVS, and are minimally affected by wildfire.

We estimated the carbon contained in live and dead trees with the Western Sierra variant of FVS (FVS, Dixon 2002). FVS uses species specific volume equations and wood density values to estimate live and dead tree biomass, and a factor of 0.5 to convert wood biomass into carbon. We used biomass equations for *Abies concolor* to estimate the carbon contained in trees which were removed during thinning, as we did not separate our stump surveys by species, and *Abies concolor* was the most commonly removed tree species.

We estimated the carbon content of surface fuels (FWD, CWD, litter/duff) by first estimating fuel biomass using conventional methods and then converting biomass into carbon using a factor of 0.5 for woody fuels, and 0.37 for litter and duff (Penman, 2003). Biomass of FWD was estimated using techniques set forth in Brown (1974), using published estimates of average piece diameter and secant, averaged for Jeffrey pine and white fir fuelbeds (van Wagendonk et al., 1998). Biomass of CWD was estimated as per Waddell (2002). Litter and duff biomass was estimated using published allometries relating litter duff biomass as a simple function of depth. We averaged the co-efficients for *P. jeffreyi* and *A. concolor* fuelbeds, coming up with the equation: where BM_{LD} is biomass of litter/duff in kg m^{-2} and depth is measured in cm (van Wagendonk et al., 1996).

2.0 Sensitivity analysis

2.1 Additional description of mortality scenarios:

We developed five different mortality scenarios using field based estimates of tree mortality rates by diameter class to define each scenario. We recognize that fires which kill more trees will also likely consume a greater proportion of existing biomass. We attempted to account for this by using a simple set of combustion co-efficients to model increasing consumption of surface carbon pools by more intense fire. We used estimates of combustion rates by carbon pool from Campbell et al (2007) as the basis for our simple model (Appendix Table 1).

Mortality Scenario	% LD consumed	% FWD consumed	% CWD consumed
1	0.6	0.6	0.4
2	0.7	0.7	0.5
3	0.8	0.8	0.6
4	0.9	0.9	0.7
5	1.0	1.0	0.8

Appendix A Table 1. Combustion rates as a percentage of pre-fire mass for litter and duff (LD), fine woody debris <7.62 cm diameter (FWD) and coarse woody debris > 7.62 cm diameter (CWD), for mortality scenarios 1-5. Values based on Campbell et al. (2007).

2.2 Additional description of regeneration scenarios

Although we only present results from our most simple regeneration model, we also examined how using a more sophisticated regeneration model might influence our results.

In the model we presented (regeneration model A), we simulated five different densities of regeneration (1400, 1005, 670, 335, and 165 seedlings ha-1) immediately after fire, splitting seedlings between Jeffrey pine and white fir, and did not add additional regeneration throughout the modeling period. Although this model results in a range of forest densities, it does not account for the impact of continued regeneration upon time scales of recovery.

We developed two additional regeneration models (models B and C) that use the same 5 rates of post-fire regeneration used in model *A* (165 to 1400 seedlings ha-1) in the first 20 years after fire, but also add additional regeneration throughout the modeling period. In models B and C, initial regeneration is prolonged over 20 years, with 50% of regeneration applied in year 1 after fire, 25% in year 5, 15% in year 10, and 10% in year 20.

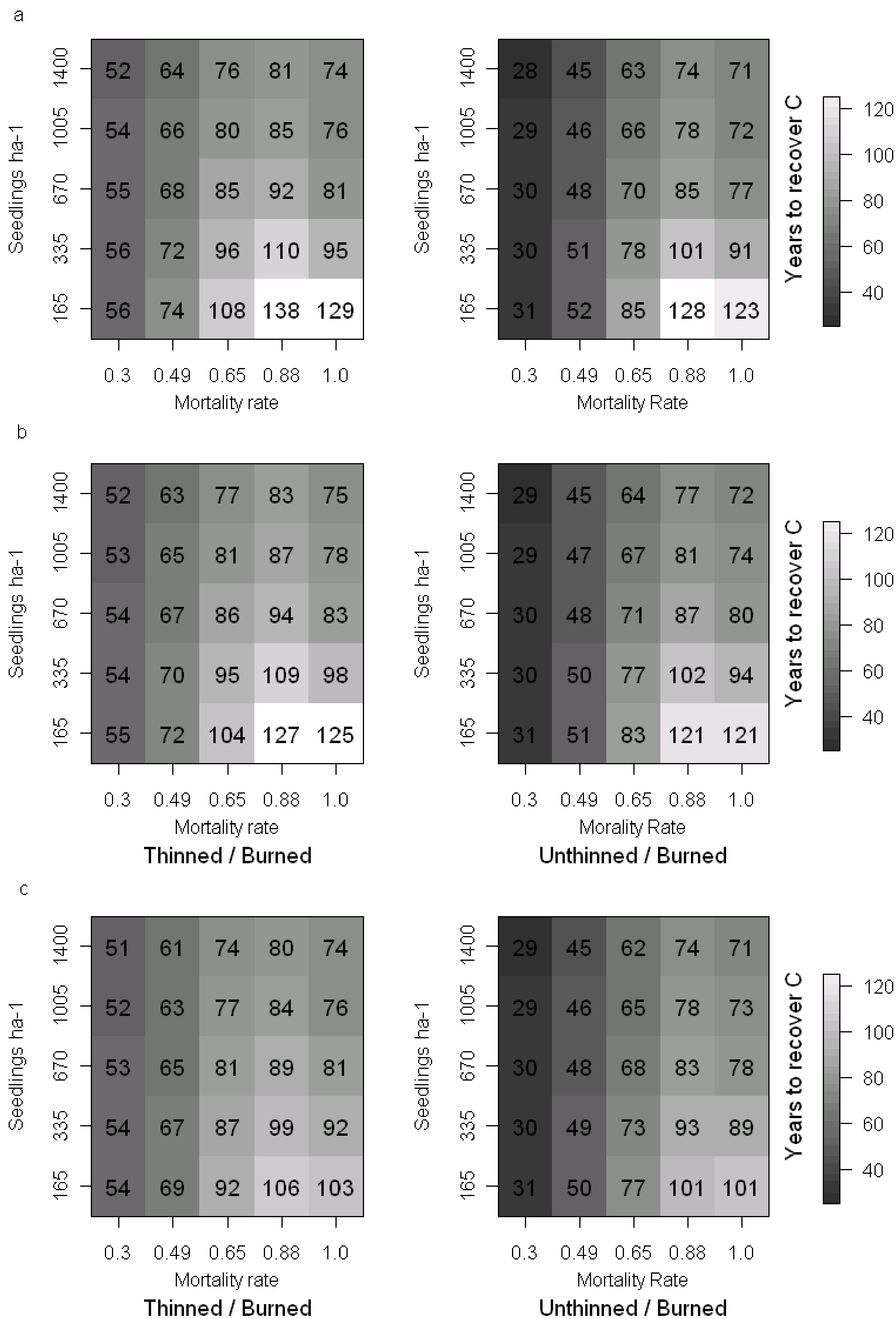
In regeneration model B, continuing regeneration is based on the basal area of Jeffrey pine and white fir in the simulated stand. Every decade starting 20 years after fire, we added 300 white fir seedlings ha-1 per m2 ha-1 basal area of mature white fir in the stand, and 100 Jeffrey pine seedlings ha-1 per unit basal area mature of Jeffrey pine, values based on mean seedling establishment rates per pre-fire basal area of these two species in our study area (data not shown). Survival rates were set as 5% and 10% for *A. concolor* and *P. jeffreyi*, similar to rates reported in the literature (Zald et al., 2008). In this model, stands which experienced a lower fire-related mortality received more continuing regeneration, due to the higher basal area of mature trees (i.e. 'rich get richer' regeneration model).

In regeneration model C, we simulate regeneration as a fixed decadal amount, regardless of overstory basal area, adding 300 white fir and 100 Jeffrey pine seedlings every 10 years starting 20 years after fire, with a 100% survival rate.

2.3 Impact of using different regeneration models on sensitivity results:

Using regeneration model B in our sensitivity analysis, we predicted similar time scales of recovery for most combinations of regeneration and mortality. In simulations where where mortality was high, and initial regeneration low, the use of Regen model B bresulted in carbon recovery about 10 years faster than in our simplest model. (Appendix A Figure 1).

Regeneration model C added significantly more regeneration throughout the modeling period than either model A or B (161.9 trees ha-1 decade-1 after 20 years). Using this model did not significantly change our results. In simulations where where mortality was high, and initial regeneration low, the use of Regen model C resulted in carbon recovery about 25 years faster than in our simplest model. However, initially low regeneration still clearly influences time scales of recovery, and mortality becomes an even more dominant of a driver of time scales of recovery (Figure 1).



Figures 1a-1c. Sensitivity results using regeneration model A, B, and C.

3.0 Forest Vegetation Simulator Settings

3.1 Wildfire modeling

We used the Fire and Fuels extension to FVS (FVS-FFE, Reinhardt and Crookston 2003) as a tool to compare how estimates of carbon recovery after disturbance might differ when using modeled versus observed tree mortality at our study site. We simulated wildfire in treated and untreated stand, using reconstructions of pre-fire conditions, and fire weather conditions observed during the Angora wildfire. Murphy et al. (2007) report that on the day that the Angora fire ignited, large dead fuel moisture was 9%, life woody fuel moisture was 73%, minimum relative humidity was 8%, and wind gusts ranged from 5 to 22 miles per hour, with firefighters reporting stronger gusts. FVS-FFE requires more inputs regarding fuel moisture and fire weather than were reported by Murphy et al. (2007). We used the following parameter settings in our wildfire simulation, using defaults for “severe” wildfire where published estimates were not available (Appendix A Table 2).

Parameter	Value
Windspeed	20 mph
1 hr (% moisture)	10
10 hr (% moisture)	10
100 hr (% moisture)	10
3”+ (% moisture)	9
Duff (% moisture)	152
Live woody (% moisture)	73
Live herb (% moisture)	150

3.2 Forest growth modeling

We used appropriate default FVS settings for our study site. We used a site index of 50, an elevation of 6500 ft, and selected Jeffrey pine as a site species. We used annual decay rates of 0.25 for litter, 0.002 for duff, 0.025 for fuels 0-4.62 cm diameter, and 0.013 for fuels >4.62 cm diameter (FVS-WS defaults). When we added post-fire regeneration using the PLANT keyword, we used a 100% establishment rate (any mortality was simulated by the density dependant model).

Appendix B. Additional regeneration statistics

Species	Year Establishing	Planted / Natural	Statistic	Treated Stands (n=37)	Untreated Stands (n=71)
Pinus jeffreyi	2009	N	Mean	60.77	36.54
			Sd	204.73	120.25
			Median	0.00	0.00
	2010	N	Mean	444.12	155.92
			Sd	725.37	368.86
			Median	172.97	0.00
	2010	P	Mean	28.05	104.76
			Sd	125.75	232.95
			Median	0.00	0.00
Pinus lambertiana	2009	N	Mean	0.00	0.00
			Sd	0.00	0.00
			Median	0.00	0.00
	2010	N	Mean	0.00	24.36
			Sd	0.00	166.16
			Median	0.00	0.00
	2010	P	Mean	28.05	17.05
			Sd	170.62	66.38
			Median	0.00	0.00
Calocedrus decurrens	2009	N	Mean	9.35	1130.42
			Sd	56.87	9442.16
			Median	0.00	0.00
	2010	N	Mean	18.70	2.44
			Sd	113.75	20.53
			Median	0.00	0.00
	2010	P	Mean	9.35	26.80
			Sd	56.87	111.90
			Median	0.00	0.00
Abies concolor	2009	N	Mean	116.87	784.47
			Sd	307.96	3985.14
			Median	0.00	0.00
	2010	N	Mean	0.00	0.00
			Sd	0.00	0.00
			Median	0.00	0.00
Abies magnifica	2009	N	Mean	107.52	484.81
			Sd	324.51	3717.08
			Median	0.00	0.00
	2010	N	Mean	0.00	0.00
			Sd	0.00	0.00
			Median	0.00	0.00