FINAL REPORT

Title: Effects of climate change and climate-altered
fire regimes on whitebark pine populations

JFSP PROJECT ID: 16-2-01-13

FEBRUARY 2018

Diana F. Tomback
University of Colorado Denver

Elizabeth R. Pansing
University of Colorado Denver

FIRESCIENCE.GOV
Research Supporting Sound Decisions

Table of Contents

List of Tables

List of Figures

List of Abbreviations/Acronyms

GYE	Greater Yellowstone Ecosystem
IGBST	Interagency Grizzly Bear Study Team
JFSP	Joint Fire Sciences Program

Keywords

Whitebark pine, climate change, fire return interval, extinction risk, stochastic demographic model

Acknowledgements

Abstract

As climate change alters global fire regimes, fire and forest managers must prioritize management actions that simultaneously protect sensitive resources and allow fire to maintain its ecological role. Over the last twenty years, this task has become more difficult, as increased fire severity and season length have caused suppression costs to rise from 16 to 52% of the USFS annual budget, limiting funding for other agency projects (USFS 2015). Further, climate change is expected to be cause increased fire frequency, severity, and area burned, exacerbating budgetary uncertainty and highlighting the need to prioritize management actions and ensure funds are used efficiently.

Whitebark pine (*Pinus albicaulis*) is a widely distributed subalpine and treeline species of management concern in the western U.S that relies on high severity burns to create early seral communities that favor its regeneration, but wildfire may also kill mature whitebark pine in absence of protective actions to prevent mortality. Management using wildland fire, or mid- to high-severity prescribed burns therefore prioritize regeneration opportunities over mature tree persistence. However, empirical analyses demonstrating the relative importance of regeneration vs. mature trees to population growth are lacking. Additionally, reductions in fire return interval, which are predicted to occur as the climate warms (from >120 to <30 years in the GYE), increase the risk of population extinction. We do not yet understand the impact of these novel fire regimes on whitebark pine population extinction risk and population dynamics.

We created a stochastic stage-based projection model to investigate the effect of decreasing fire return intervals on the probability of extinction and time to extinction of a whitebark pine population. This projection model relies on demographic data collected intermittently from 1990 to 2017 from whitebark pine communities recovering from the 1988 Yellowstone fires and contiguous unburned locations, and values obtained from the literature. We projected whitebark pine population size 500 years into the future 10,000 times considering the effects of fire return intervals decreasing from > 200 years to < 30 years by 2100. We used these projected population sizes to estimate population density at each time step, probability of population extinction, average time to population extinction, and the stochastic growth rate. We also estimated the contribution of each survival and transition rate to the overall population growth (i.e., stochastic elasticity) to determine whether protecting mature trees or promoting regeneration would benefit whitebark pine population growth as fire regimes change.

As originally proposed, the model structure does not sufficiently describe whitebark pine population dynamics, and results in unrealistically high population densities (maximum projected density over 10,000 iterations = 6.79e+89 trees/ m^2). We estimated stochastic lambda to be 1.12, or 12% growth per year. The original proposal and literature lack an understanding of the specific nature and timing of density-dependent factors that restrict whitebark recruitment and growth in successional communities, but the 1990 to 2017 post-fire dataset may provide insight into these effects in the developing community. In light of our initial results, we are expanding the model to incorporate density-dependent effects including the effects of canopy closure on germination and seedling survival, variation in seed dispersal rates as seed production fluctuates, the relationship between cone production and predispersal cone predation, and the increase in post-dispersal seed predation with time since fire. To begin, we incorporated the effects of canopy closure on germination and cone crop size on seed dispersal. Management recommendations will be made when the final model incorporating density-dependent effects is completed.

Objectives

Objective 1: Estimate cone crop size and seed survival rates. Cone crop data allows estimation of survival probability of cones persisting on a tree until dispersal begins; the major factors in declining cone numbers are squirrel predation and pre-dispersal foraging by nutcrackers. This transition probability is one of the few in the whitebark pine life cycle that still requires estimation. This vital rate was to be incorporated into the stage-specific projection matrix model to estimate life stage elasticities and extinction risk.

This objective was not achieved because cone production during the funded field season was nearly zero, which precluded our ability to estimate cone and seed survival rates. We instead used annual cone production data obtained from the IGBST (Haroldson 2017), which has collected these data from around the GYE since 1980 from permanent transects. Although these data were not collected from our study locations, they represent a general average for the ecosystem.

We estimated predispersal predation rates using information from McKinney and Tomback (2007), who estimated the proportion of cones removed from trees by seed predators, including red squirrels, as a function of cone availability. Although these estimates are not specific to the GYE, they are the only empirical estimates of cone survival in the literature.

Objective 2: Create a stochastic stage-based projection matrix to estimate life-stage elasticities based on current fire regimes and determine the impact of decreasing fire return intervals on extinction risk and elasticities. A stage-based projection matrix model for whitebark pine will be developed and used for subsequent analyses. Stage-based projection matrix models are commonly used for elasticity analyses that have helped identify appropriate management actions in other species (Crowder et al. 1994, Crooks et al. 1998). Estimating the effect of climate-altered fire regimes on extinction risk and sensitive life stages will allow managers to prioritize management strategies that favor life stages with the greatest influence on population growth rates, and project how changes to the fire regime will perturb population dynamics.

Objective 3: Suggest fire management strategies that prioritize whitebark pine life stages with the largest effect on population growth rates (i.e., highest elasticities) to minimize extinction risk resulting from future fire regimes. Model results will be interpreted to devise realistic restoration and management goals that will enable managers to maintain whitebark pine populations.

Although objective 2 was successfully implemented, results indicate that the model structure originally proposed to JFSP was insufficient to capture the population dynamics of whitebark pine in the GYE. We are taking steps towards improving the model structure to provide concrete management recommendations.

Background

Climate change is expected to drastically alter the timing, frequency, intensity, and spatial extent of disturbances (Dale et al. 2001, Lenihan et al. 2008, Donato et al. 2009, Westerling et al. 2011, Westerling 2016). Temperate coniferous forests in the Northern Rocky Mountains of the United States, which are adapted to stand replacing fires, are experiencing higher temperatures, drier summers, reduced winter precipitation, and earlier snowmelt (Westerling et al. 2006, Donato et al. 2009, Dennison et al. 2014, Millar and Stephenson 2015, Harvey et al. 2016, Kemp et al. 2016, Rother and Veblen 2016, Westerling 2016, Stevens-Rumann et al. 2017). As a result, fire regimes in the Northern Rockies have changed substantially in the last quarter century, and

changes are expected to continue as climate change progresses (Westerling et al. 2006, Abatzoglou and Williams 2016, Westerling 2016). By the late 21st century, fire rotation time is projected to decrease from > 100 years to < 30 years, and annual area burned is expected to increase to more than 100,000 ha annually by 2050 (Westerling et al. 2011). These novel fire regimes, in conjunction with climate-induced changes to demographic processes, are hypothesized to result in "interval squeeze" and increase the likelihood of population extirpation and/or extinction, and ecosystem state changes (e.g., transition from forest to grassland; Enright et al. 2015).

The chances of extirpation are expected to be particularly pronounced for slow growing species that require decades to reach reproductive maturity (Westerling et al. 2011, Enright et al. 2015), but direct studies of these processes are difficult because of long generation times. In these cases, models are useful for understanding potential outcomes of different hypotheses. Further, although independent studies suggest associations among water stress, distance to seed source and recruitment, and between fire regime shifts and altered demographic processes, we are not aware of any study that investigates the effects of altered fire on extinction probability. We created a stage-based projection model to assess how changing fire regimes might influence the probability of extinction and time to extinction using a long-lived species of management concern.

Whitebark pine (*Pinus albicaulis*), which is widely distributed throughout subalpine and treeline forest zones of the western United States, acts as a foundation and keystone species by defining ecosystem structure and fostering biodiversity (Tomback et al. 2001a, Ellison et al. 2005, Tomback and Achuff 2010). However, this iconic species is at risk and currently under evaluation for listing under the Endangered Species Act (USFWS 2011). The key causes cited for declines include widespread damage and mortality from an invasive fungal pathogen (*Cronartium ribicola*) that causes white pine blister rust, and large-scale outbreaks of mountain pine beetle (*Dendroctonas ponderosae* ;Tomback et al. 2001a, Kendall and Keane 2001, Tomback and Achuff 2010, Schwandt et al. 2010). Whitebark pine is a long-lived (up to 1200 years; Perkins and Swetnam 1996) species that first reaches reproductive maturity at 30 years, in contrast to its common conspecifics lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), which can produce seed cones at fewer than 10, 15, and 20 years of age, respectively (Lotan and Perry 1983, Alexander and Shepperd 1984, Alexander et al. 1984). The natural history of successional whitebark pine communities is integrally tied to fire; whitebark pine is a pioneer species that regenerates quickly after fire because its seeds are dispersed long distances by its avian seed disperser, Clark's nutcracker (*Nucifraga columbiana*). Furthermore, whitebark pine seedlings tolerate harsh seedbeds and conditions better than competitors (Tomback 1982, 2005,McCaughey and Tomback 2001, Lorenz et al. 2011). On productive sites in its Rocky Mountain range, whitebark pine relies on fire to open sites for seed dispersal and regeneration, slow succession, and reduce the density of faster-growing, shade-tolerant conifers that would replace whitebark pine in absence of fire (Arno 1980, Arno and Hoff 1989).

As fire regimes change, the infrequent high severity burns that promote whitebark pine regeneration and postpone successional advance will transition to more frequent high severity burns, potentially threatening the persistence of this foundation species. Fire managers must prioritize management actions that simultaneously protect sensitive resources and allow fire to maintain its ecological role. Over the last twenty years, this task has become more difficult, as increased fire severity and season length have caused suppression costs to rise (USFS 2015).

However, guidance to protect certain populations can be written into National Forest Plans, if a management strategy has been devised. Climate change is expected to lead to increased fire frequency, severity, and area burned, exacerbating budgetary uncertainty and highlighting the need to prioritize management actions and ensure funds are used efficiently.

To understand the impact of novel fire regimes on whitebark pine extinction risk and population dynamics, we created a population projection model of a whitebark pine population to estimate the probability of and time to population extinction, and to identify the life stages with the greatest impact on population growth and extinction risk at current and predicted future fire return intervals. This stochastic stage-based projection model relies on demographic data collected intermittently from 1990 to 2017 (Tomback et al. unpublished data) from whitebark pine communities recovering from the 1988 Yellowstone fires and unburned locations in the Greater Yellowstone Ecosystem (GYE), an ecosystem where the effects of climate on fire have been well-investigated (e.g., Westerling et al. 2011, Westerling 2016). We projected whitebark pine population size 500 years into the future to determine how the effects of decreasing fire return intervals will influence the probability of extinction and time to extinction.

Although we acknowledge that the impacts of both white pine blister rust and mountain pine beetle outbreaks on whitebark pine populations have been, and will continue to be, substantial, here we focus on determining the effects of decreased fire return intervals on vital rates. We intend that this modeling effort will provide clear guidance about population responses and provide strategies for mitigating potential negative consequences of altered fire regimes.

Materials and methods

Demographic projection models are a useful tool for "projecting" population sizes forward in time to estimate population growth rates based on empirically estimated survival probabilities. These models can be extended to stage- or age-structured populations. We apply this modeling framework to investigate the effects of climate-caused decreases in fire return intervals on a 38.6 square mile (10,000 ha) whitebark pine population, incorporating annual stochasticity into demographic processes to account for variability in demographic rates. We consider the whitebark pine life cycle to be comprised of six distinct life stages.

Whitebark pine life cycle

We define the whitebark pine life-cycle as a six life-stage process comprised of first year seeds (*SEED1*), second year seeds (*SEED2*), first year seedlings (*SD1*), seedlings (*SD*), saplings (*SAP*), and mature adults (*MA*; Figure 1).

First-year seeds (SEED1)

We divide the seed stage into two distinct life stages because whitebark pine forms a persistent soil seedbank; germination often occurs after one to several years in the soil (Tomback et al. 2001b, Tillman-Sutela et al. 2008). We considered first year seeds to be newly dispersed from mature trees and have been in the soil for less than one year. We assume that the fate of first-year seeds is to either 1) persist as a component of the soil seed bank (i.e., the probability of the SEED1 stage transitioning to the SEED2 stage; $t_{SEED1-SEED2}$), germinate (i.e., probability of transitioning from the SEED1 stage to the SD stage; $t_{SEED1-SD}$), or 3) die. Seed mortality includes inviable and moldy seeds, and seed pilferage by granivorous rodents (Pansing et al. 2017). Persistence in the SEED1 stage was assumed to be zero as all seeds remaining in the soil seed bank transition to the SEED2 stage. Estimates of the probability of seed survival ($t_{SEED1-SEED2}$) and germination ($t_{SEED1-SD}$) were obtained using data from Pansing et al. (2017).
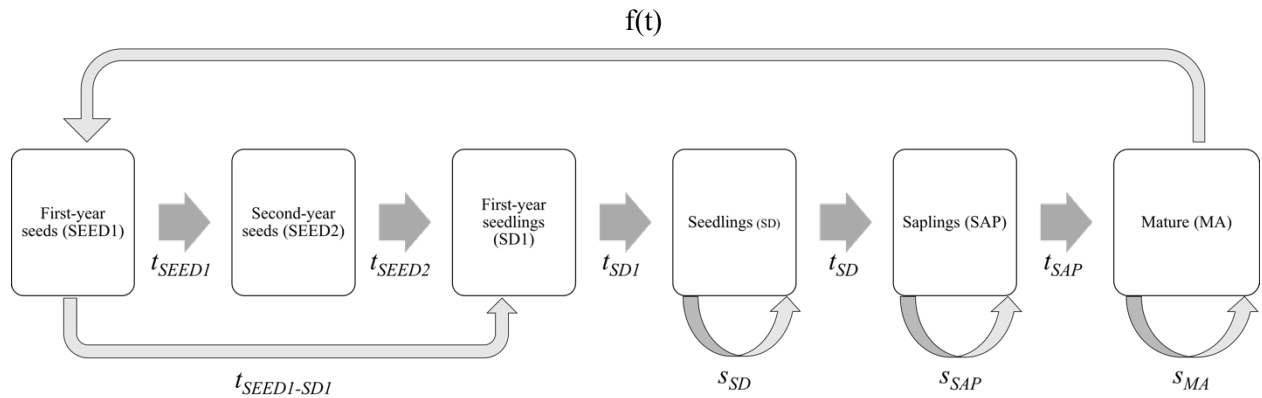
Figure 1: Life cycle of whitebark pine showing life stages used to create the stochastic projection models. Arrows represent the progression through the life cycle. t_{SEED1}: persistence of dispersed seeds in the soil seedbank; $t_{SEED1-SD1}$: germination of first year seeds; t_{SD1}, successful transition of first year seedlings to the seedling life stage; s_{SD}, survival of seedlings that remain in the seedling stage; t_{SD1}, successful transition of seedlings to the sapling life stage; s_{SAP}, survival of saplings that remain in the sapling stage; t_{SAP}, successful transition of saplings into the mature life stage; s_{MA}, survival of mature trees; f(t) describes the time dependent function that determines the number of seeds cached each year.

Second-year seeds (SEED2)

We differentiate the two seed stages because the probability of seed germination differs substantially from the first to second year in the seed bank (Tomback et al. 2001b, Pansing et al. 2017). To simplify this model, we assume second-year seeds either 1) germinate ($t_{SEED2-SD}$) or 2) die, reflecting the assumption that seeds can persist in the soil seed bank for a maximum of 2 years (i.e., all seed germination occurs during the first two years). The germination probability of second year seeds was estimated using data from Pansing et al. (2017).

First year seedlings (SD1)

Seed germination usually occurs as a result of snowmelt or rain during late spring and summer months (Tomback et al. 2001b, McCaughey et al. 1994). First year seedlings are recently germinated, usually with no adult foliage (five-needle fascicles) and have not yet experienced winter. We considered first-year seedlings distinct from other seedlings because survival rates decrease substantially after the first winter (Pansing, personal observation). First-year seedlings could either 1) survive and transition to the seedling stage (t_{SD1-SD}), or 2) die. Therefore, survival and persistence in the SD stage is assumed to be zero. We estimated the survival probability of first-year seedlings using data from Pansing et al. (2017).

Seedlings (SD)

We designated seedlings as individuals one year of age until the average age that trees reach DBH height (diameter at breast height, or 1.37 m). On average, whitebark pine in post-fire areas reach 1.37 m in height at 29 years of age (Tomback et al. 1993), and we therefore assigned the seedling class to be from age 1-29 years of age. Seedlings could either 1) survive and persist in the seedling stage (S_{SD}), 2) survive and transition to the sapling stage ($t_{SD1-SAP}$), or 3) die. Survival probabilities were estimated using data obtained from post-fire plots established in 1990 by Diana Tomback in areas affected by the 1988 Yellowstone Fires (see Tomback et al. 2001b for detailed methods). Tomback and colleagues thoroughly surveyed plots in 1990-1992, 1994, 1995, 2001, and 2016/2017 and followed individual whitebark pine trees through time, allowing us to estimate annual survival of whitebark pine seedlings (Pansing et al. in prep).

Saplings (SAP)

Saplings, as defined here, represent the life stage between trees reaching 1.37 m in height until the time trees first produce seed cones. In whitebark pine, reproductive maturity occurs between 30 and 50 years (McCaughey and Tomback 2001), although large cone crops are not generally produced until sufficient canopy development at 60-80 years of age. We therefore defined saplings as trees aged from 29 to 40 years (the average age of reproductive maturity). We have not found empirically derived survival probabilities of whitebark pine saplings, and trees in the Yellowstone fire plots are not old enough to estimate survival probabilities. Therefore, we rely on the constant survival rate used by Ettl and Cottone (2004) and Field et al. (2012) when modeling whitebark pine populations. Possible outcomes for saplings in each year were 1) survive and persist in the sapling stage (S_{SAP}), 2) survive and transition to the mature stage (t_{SAP-MA}), or 3) die.

Mature (MA)

Because cone production generally begins in whitebark pine between 30 and 50 years of age (McCaughey & Tomback 2001), we assume trees become reproductively mature (MA stage) at 40 years of age. We assume constant 1% annual mortality for this life stage. Although empirical support for this figure is lacking, and whitebark pines can live past 50 years of age, approximately the time span of interest in this modeling effort. Further, we are not interested in the impact of pests and pathogens on population dynamics and instead focus on the demographic consequences decreasing fire return intervals. Mature trees could either 1) survive and persist in the same life stage (S_{MA}), or 2) die.

Survival and Transition Rates

We have empirically derived estimates of survival probabilities for the SD stage (i.e., s_{SD}, persistence in the seedling stage), and transition probabilities for the SEED1, SEED2, and SD stages (i.e., $t_{SEED1-SEED2}$, persistence of first year seeds in the soil seed bank; $t_{SEED1-SD}$, germination of first year seeds; $t_{SEED2-SD}$, germination of second year seeds; t_{SD-SD1}, survival of newly germinated individuals that enter the seedling stage; Tomback et al. 2001, Pansing et al. 2017, Pansing et al. in prep). The remaining survival and transition probabilities are estimated using the following equations from Field et al. (2012):

$$s_i = \left(1 - \frac{1}{R_i}\right)s_i, \qquad i = SD1, SAP, MA \tag{1}$$

where s_i and t_k represent survival and transition probabilities, respectively, and R_i represents

$$t_k = \frac{1}{R_i} * s_i, \qquad k = SD1 - SAP, SAP - MA \tag{2}$$

the life stage specific residence time (i.e., time an individual persists in any given life stage). These residence times are described in the section titled "Whitebark pine life cycle", where life stage characteristics are described. Note that, as defined, the survivorship probability is contained within the transition probability (i.e., t_i includes the probability that an individual survives and transitions to life stage $i +1$; Field et al. 2012).

Fecundity

Whitebark pine has an uncommon recruitment process, and we treat fecundity as a combination of seed production and successful dispersal. Whitebark pine is a masting species, characterized by synchronous and episodic cone production (Kelly and Sork 2002, Crone et al. 2011). Large cone crops generally occur approximately every 3-5 years (Krugman and Jenkinson 1974). Whitebark pine cones are indehiscent—unlike many conifers their cone scales do not open and seeds cannot escape the cone without assistance. Seed dispersal is primarily accomplished by the Clark's nutcracker (*Nucifraga columbiana*). In late summer and fall, birds

remove cone scales to access seeds and disperse them in caches (clusters of seeds buried beneath several centimenters of substrate) across the landscape (Tomback 1978, 1982, Hutchins and Lanner 1982). The number of cones available is largely limited by pre-dispersal cone predation by red squirrels (*Tamasciurius* hudsoniscus; McKinney and Tomback 2007). Nutcrackers disperse seeds up to 32 km from the parent tree and distribute seeds in caches comprised of 1-15 seeds (Tomback 1978, 1982, Hutchins and Lanner 1982, Lorenz et al. 2011). Nutcrackers will return to these caches to consume seeds from winter through spring (Tomback 1978, 1982, Hutchins and Lanner 1982). Those seeds that are not recovered by nutcrackers and survive in cache sites may contribute to forest recruitment (Tomback 1982, Pansing et al. 2017).

For our model, only mature trees can produce cones and contribute to the next generation of individuals. We describe cone production as a cosine function with a periodicity of 4 years and normally distributed error to incorporate the masting process and periodicity of cone production in the model. We use a cosine function because whitebark pine is a masting species, characterized by synchronous and episodic cone production.

$$No.\frac{cones}{tree} = 12.5cos(1.5t) + 14 + \epsilon, \qquad \epsilon \sim \mathcal{N}(0,3.5), t = 1, \ldots m \qquad (3)$$

where t is the projection year. The equation was paramaterized using the annual average number of cones per tree at transects across the Greater Yellowstone Ecosystem from 1980 to 2016 (Haroldson 2017). For any model iteration, values lower than zero were set to zero to avoid biologically impossible outcomes.

Dispersal

Because red squirrels (*Tamiasciurus* hudsoniscus) harvest a substantial portion of cones (often greater than 80%) prior to and concurrent with seed dispersal by nutcrackers (McKinney and Tomback 2007), we assume that only 20% of the original cones are available to nutcrackers to cache. We assume that there are 45 viable seeds per cone, that 3 seeds are placed in each nutcracker cache, and that 45% of the caches are not retrieved by nutcrackers (Tomback 1978, 1982, Hutchins and Lanner 1982). These assumptions provide us with an estimate of the number of caches that result from the reproductive output of one mature tree:

$$no.\frac{caches}{tree(t)} = \frac{45 * (12.5cos(1.5t) + 14 + \epsilon)}{3} * 0.2, \qquad (4)$$
$$\epsilon \sim \mathcal{N}(0,3.5), t = 1, \ldots m,$$

where the numerator represents the number of seeds per tree, and the denominator represents the number of seeds per cache and 0.2 represents the proportion of cones that are not predated by red squirrels or other predators prior to dispersal.

Generic Model

The simplest version of our model is semi-deterministic model and incorporates demographic stochasticity in recruitment but does not incorporate fire. Its general form is described as follows:

$$
\begin{pmatrix} n_{SEED1,t+1} \\ n_{SEED2,t+1} \\ n_{SD,t+1} \\ n_{SD1,t+1} \\ n_{SAP,t+1} \\ n_{MA,t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & f(t)_{MA}s_{MA} \\ t_{SEED1-SEED2} & 0 & 0 & 0 & 0 & 0 \\ t_{SEED1-SD1} & t_{SEED2-SD1} & 0 & 0 & 0 & 0 \\ 0 & 0 & t_{SD1-SD} & s_{SD} & 0 & 0 \\ 0 & 0 & 0 & t_{SD-SAP} & s_{SAP} & 0 \\ 0 & 0 & 0 & 0 & t_{SAP-MA} & s_{MA} \end{pmatrix} \begin{pmatrix} n_{SEED1,t} \\ n_{SEED2,t} \\ n_{CS,t} \\ n_{SD,t} \\ n_{SAP,t} \\ n_{MA,t} \end{pmatrix} \tag{5}
$$

Incorporating demographic stochasticity

We incorporated demographic stochasticity, variation in demographic rates resulting from chance events (Lande et al. 2003), by randomly selecting vital rates (survival and transition probabilities) from probability distributions derived from existing demographic data (Tomback et al. 2001, Pansing et al. 2017, Tomback et al. in prep, Pansing et al. in prep). We used method of moments to convert means and variances of empirically derived survival and transition probabilities to parameters describing a beta distribution (α, β). The beta distribution is a continuous probability distribution whose domain is defined on the interval [0, 1]. This conversion was required because survival and transition probabilities lie on this interval [0,1], whereas drawing from normal or binomial distributions could produce impossible values for survival and transition probabilities. During each time step, vital rates were drawn from their respective distributions to create a survival and transition matrix. Parameters and their distributional assumptions are shown in Table 1.

Parameter	Symbol	Distribution	Parameters
Seedling survival	s_{SD1}	Beta	Alpha = 12.53 Beta = 0.403
Sapling survival	s_{SAP}	Constant	0.8
Mature tree survival	s_{MA}	Constant	0.99
Persistence in soil seed bank	$t_{SEED1\ SEED2}$	Beta	Alpha = 195.86 Beta = 506.27
SEED1 germination	$t_{SEED1-SD}$	Beta	Alpha = 255.36 Beta = 480.14
SEED2 germination	$t_{SEED2-SD}$	Beta	Alpha = 193.43 Beta = 536.68
SD survival and transition to SD1	t_{SD-SD1}	Beta	Alpha = 108.61 Beta = 112.50
Residence time SD1	R_{SD1}	Constant	29
Residence time SAP	R_{SAP}	Constant	20
Residence time MA	R_{MA}	Constant	∞
No. cones per tree	C_{tree}	NA	$12.5cos(1.5t) + 14 + \epsilon,$ $\epsilon \sim \mathcal{N}(0,3.5),$ $t = 1, \dots 500$
Fire return interval	F	Gamma	Shape = 3.44 Rate = 0.015

Table 1: Parameters used in defining the structure of the model, the symbol used to describe the parameter in each equation, their distributional assumptions, and the values used to generate each parameter at each time step.

Incorporating fire and decreasing fire return intervals

We treated fire as a Markovian process with three distinct states: 1) fire occurred in the current time step ($t = t$); 2) the most recent fire occurred in the previous year ($t = t - 1$); or, 3) the most recent fire occurred two or more years prior

$(t \leq t - 2)$. The temporal distribution of time between fires is modeled as a gamma distribution, which is well suited to describe variables constrained to positive values and are generally used to describe waiting time between events of interest (Bolker 2008). Gamma parameters were estimated using method of moments, converting the mean and standard deviation of documented fire return intervals in Greater Yellowstone whitebark pine forests (Larson et al. 2009). We assumed that fires were stand-replacing (i.e., no trees in the affected subpopulation survive), and no new recruitment occurred during the fire year because these fires are usually not fully extinguished until first snowfall, and conditions are no longer suitable for germination (Romme 1982). New recruitment in the following years (until individuals in the affected subpopulation reach reproductive maturity) was assumed to be the result of dispersal from nearby populations not included in the model. Fire years were determined prior to each projection iteration by selecting years from the gamma distribution of fire intervals.

When the population is in state 1 (i.e., the current year is a fire year), the following survivorship and transition matrix is used:

$$
\begin{pmatrix} n_{SEED1,t+1} \\ n_{SEED2,t+1} \\ n_{SD,t+1} \\ n_{SD1,t+1} \\ n_{SAP,t+1} \\ n_{MA,t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} n_{SEED1,t} \\ n_{SEED2,t} \\ n_{CS,t} \\ n_{SD,t} \\ n_{SAP,t} \\ n_{MA,t} \end{pmatrix}
\tag{6}
$$

indicating that all trees are dead, and no recruitment occurs.

When the system is in state 2, the following matrix is used:

$$
\begin{pmatrix} n_{SEED1,t+1} \\ n_{SEED2,t+1} \\ n_{SD,t+1} \\ n_{SD1,t+1} \\ n_{SAP,t+1} \\ n_{MA,t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 50*f(t) \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} n_{SEED1,t} \\ n_{SEED2,t} \\ n_{CS,t} \\ n_{SD,t} \\ n_{SAP,t} \\ n_{MA,t} \end{pmatrix}
\tag{7}
$$

indicating that recruitment can only occur as a result of seed dispersal from outside populations. We assume that the cone production function in the nearby population operates the same as that of our target population and that the caches resulting from 50 trees are input into the population, where the number of trees providing seeds to the system was back calculated using the number of individuals that germinated in a given year, the germination and cache pilferage rates reported by Pansing et al. (2017), and the average number of seeds per cache and seeds per cone (Tomback 1982). In state 3, the matrix presented in equation 5 is used.

Projecting population size forward in time

After incorporating fire and climate effects on recruitment (see sections below), we projected whitebark pine populations forward in time, using population size at time t to project population size at time $t+1$. We projected populations sizes out 500 years and conducted 10,000 iterations of the simulation to obtain uncertainty estimates. For each iteration, we tracked annual population sizes for each life stage. Total annual population sizes were calculated excluding seed stages, as most population assessments of plants do not include seed counts. We then convert the population size to density (no./m^2).

After completing 10,000 iterations, we calculated the proportion of iterations for which the population size decreased to zero and stayed at zero for the remainder of the projection time

(i.e., population extinction occurred). We then calculated the stochastic population growth rate (stochastic lambda), and stochastic elasticity using Tuljapurkar's approximation (Caswell 2001).

Results and Discussion

We projected population sizes forward 10,000 times. The average maximum population density across all iterations was 2.03e+85 whitebark pine trees/m^2, with a maximum of 6.79e+89 trees/ m^2 (Figure 2). We estimated a stochastic lambda of 1.12, or a growth rate of, on average, 12% per year. These results indicate that the proposed model structure is insufficient to capture realistic population dynamics occurring in whitebark pine populations in the GYE, as average densities of whitebark pine in the GYE have been estimated to be 0.00375 trees/m^2 (Tomback et al., in prep).
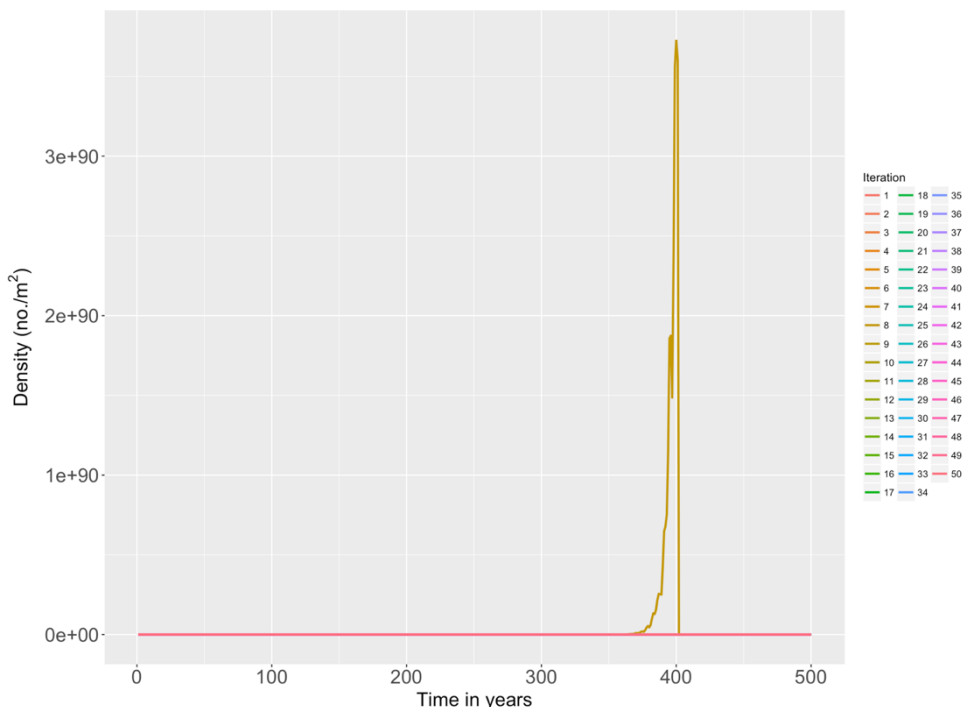

Figure 2: Density (no. trees/m^2) at each time step for 50 of 10,000 iterations. Densities were projected out 500 years. Each color represents a different iteration of the model. The sharp decline of density to zero represents a fire event.

Of the 10,000 model iterations, populations experienced permanent extinction 7.26% of the time (95% CI: 6.76, 7.79), suggesting that population extinctions would be quite rare even in as fire return intervals decrease, if 3e90 trees/m^2 were a reasonable prediction of future population densities. However, these results cannot be used because of model limitations, which we plan to overcome (see below).

Science delivery activities

We have submitted an abstract to present an advanced version of this model at the ESA 2018 conference in New Orleans, LA. The work will additionally be submitted for publication once the model structure has been modified and results better reflect observed densities of whitebark pine populations (see the section entitled "Incorporating density dependent effects" for plans to modify the model). Additionally, the model itself will be distributed to the Joint Fire Sciences Program for distribution to land managers who have estimated demographic rates for whitebark

pine and would like to use the model to understand the potential effects of decreased fire return intervals on their specific management units.

Conclusions, Implications for Management and Future Research

At this juncture, we hesitate to provide management recommendations until the model structure can be further refined to produce densities in line with those reported in the literature. Because answering the questions we posed is an important step towards prioritizing management actions as fire regimes shift in response to climate change, we are working to refine the structure of our model to ensure that it better reflects observed population dynamics. Once we obtain results from our improved model, we will report the findings, management recommendations, and model itself to the Joint Fire Sciences Program.

Incorporating density dependent effects

Once we determined that the model structure we proposed did not result in realistic population dynamics, we have moved forward to incorporate density-dependent effects to regulate seed dispersal, germination, and seedling survival.

We have successfully incorporated both the effects of increased shading and canopy closure on germination rates, as well as increasing the effects of increased cone production on nutcracker caching (see Field et al. 2012, Figure 1, Eqs. 22-30). The incorporation of these two density dependent effects has substantially altered the behavior of the model (Figure 3), reducing the average density to 1.32e-4 trees/m^2 and the maximum density to 1.54e-4 trees/m^2.
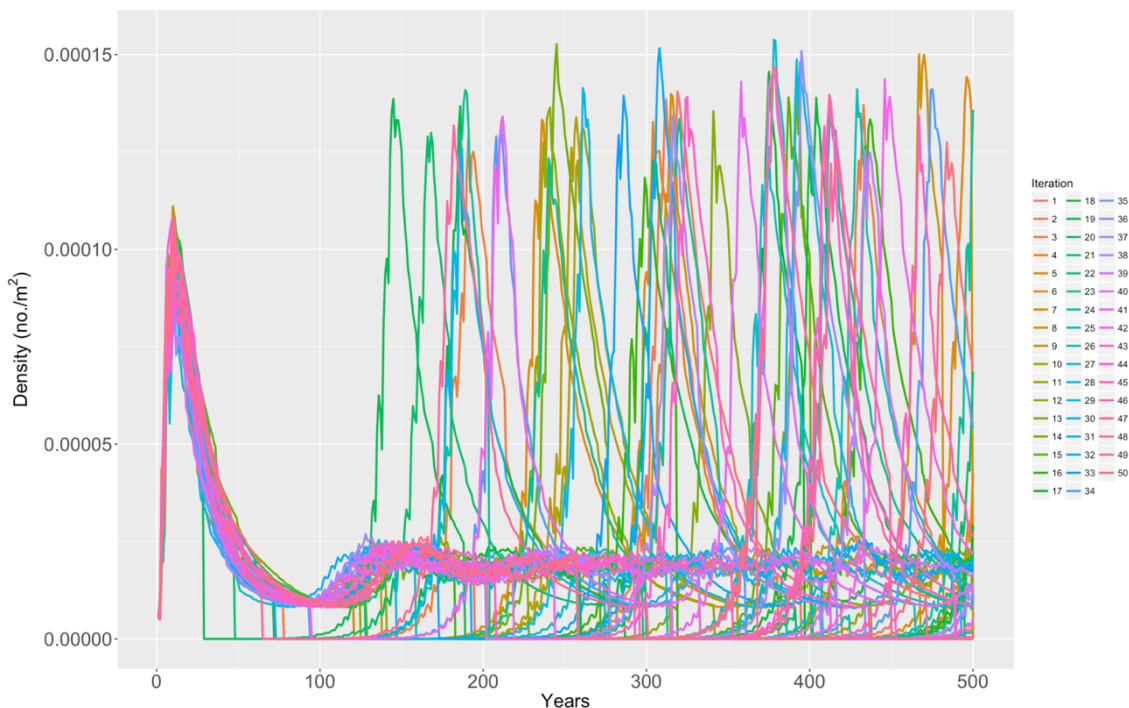

Figure 3: Whitebark pine density (no. trees/m2) over time for 50 model runs after incorporating the effects of canopy closure on germination, and of cone production on the proportion of seeds cached by nutcrackers. Each vertical line where density drops to zero represents a fire event.

Other density dependent effects that will be incorporated include varying the proportion of cones that are predated prior to dispersal (i.e., as cone production increases, the relative

proportion of cones removed by seed predators decreases; McKinney and Tomback 2007) and varying the proportion of caches eaten by small mammals following dispersal in response to changing rodent abundance following fire (e.g., Fisher and Wilkinson 2005, Zwolak et al. 2010).

The empirical data we collected have been immensely useful for calibrating this projection model. Our goal is first to obtain a realistic demographic projection model that includes natural processes that lead to density-dependent effects. After incorporating these changes, we will revisit the effects of decreasing fire return intervals and devise management recommendations. We intend to share this information with the JFSP in the form of a draft manuscript as a follow up report.

References

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113:11770–11775.

Alexander, R. R., and W. D. Shepperd. 1984. Silvicultural Characteristics of Engelmann Spruce.

Alexander, Robert R.; Shearer, Raymond C.; Shepperd, Wayne D. 1984. Silvical characteristics of subalpine fir. Gen. Tech. Rep. RM-115. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 29 p.

Arno, S. F. 1980. Forest fire history in the Northern Rockies. Journal of Forestry 78:460–465.

Arno, S. F., and R. J. Hoff. 1989. Silvics of whitebark pine (Pinus albicaulis). General Technical Report Intermountain Research Station, USDA Forest Service No. INT-25:11 pp.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press. Princeton, New Jersey, USA.

H. Caswell. 2001. Population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Crone, E. E., E. J. B. McIntire, and J. Brodie. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. Journal of Ecology 99:438–444.

Crooks, C. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. Conservation Biology 12:889-895.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994 Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4: 437-445.

Dale, V., L. Joyce, S. Mcnulty, R. Neilson, M. Ayres, M. Flannigan, P. Hanson, L. Irland, A. Lugo, C. Peterson, D. Simberloff, F. Swanson, B. Stocks, and M. W. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. a. Moritz. 2014. Geophysical Research Letters. Geophysical Prospecting 41:2928–2933.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. a. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. a. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. a. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Enright, N. J., J. B. Fontaine, D. M. J. S. Bowman, R. A. Bradstock, and R. J. Williams. 2015.

Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Frontiers in Ecology and the Environment 13:265–272.

Ettl, G., and N. Cottone. 2004. Whitebark pine (*Pinus albicaulis*) in Mt. Rainier National Park: response to blister rust infection. Pages 36–47 *in*: H. Akçakaya, M. Burgman, O. Kindvall, C. Wood, P. Sjögren-Gulve, J. Hatfield, and M. McCarthy, editors. Species conservation and management.Oxford University Press, New York, New York, USA.

Field, S. G., A. W. Schoettle, J. G. Klutsch, S. J. Tavener, and M. F. Antolin. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: A nonlinear disease model. Ecological Applications 22:166–183.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review, 35: 51–81. doi:10.1111/j.1365-2907.2005.00053.x

Haroldson, M. A. 2017. Whitebark pine cone production. Pages 53-55 *in* F. T. can Manan, M. A. Haroldson, and B. E. Karabensh, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2016, U.S. Geological Survey, Bozeman, Montana, USA.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.

Hutchins, A. H. E., and R. M. Lanner. 1982. The Central Role of Clark ' s Nutcracker in the Dispersal and Establishment of Whitebark Pine. Oecologia 55:192–201.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? Annual Review of Ecology and Systematics 33:427–447.

Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology 31:619–636.

Kendall, K. K., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221-242 *in*: D. F. Tomback, S. F. Arno, and R. E. Keane, eds., Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Krugman, S. L. and J. L. Jenkinson. 1974. *Pinus* L. pine. Pages 598-638 *in*: C. S. Schopmeyer, technical coordinator. Seeds of woody plants in the United States. USDA Forest Service Agriculture Handbook No. 450, Washington D.C., USA.

Lande R., S. Engen, and B-E. Sæther. 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford.

Larson, E. R., S. L. Van De Gevel, and H. D. Grissino-Mayer. 2009. Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. Ecoscience 16: 282-298.

Lenihan, J. M., D. Bachelet, R. P. Neilson, and R. Drapek. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. Climatic Change 87:215–230.

Lorenz, T. J., K. A. Sullivan, A. V. Bakian, and C. A. Aubry. 2011. Cache-site selection in Clark's nutcracker (*Nucifraga columbiana*). The Auk 128:237–247.

Lotan, J. E., and D. E. Perry. 1983. Ecology and regeneration of lodgepole pine. USDA Forest Service Ag. Handbook No. 606. Fort Collins, Colorado, USA.

McCaughey, W. W., and D. F. Tomback. 2001. The natural regeneration process. Pages 105-120

in: D. F. Tomback, S. F. Arno, and R. E. Keane, eds. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

McCaughey, W. W. 1994. The regeneration process of whitebark pine. Pages 179-187 *in*: W. C. Schmidt, and F-K. Holtmeier, eds. Proceedings: International workshop on subalpine stone pines and their environment: the status of our knowledge. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research 37: 1044-1057.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Pansing E. R, D. F. Tomback, M. B. Wunder MB, J. P. French, and A. C. Wagner. Microsite and elevation zone effects on seed pilferage, germination, and seedling survival during early whitebark pine recruitment. Ecol Evol. 2017;7:9027–9040. https://doi.org/10.1002/ece3.3421

Rother, M. T., and T. T. Veblen. 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7(12):e01594. 10.1002/ecs2.1594

Romme, W. H. 1982. Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park. Ecological Monographs, 52: 199–221. doi:10.2307/1942611

Schwandt, J. W., I. B. Lockman, J. T. Kliejunas, and J. A. Muir. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology, 40: 226–250. doi:10.1111/j.1439-0329.2010.00656.x

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol Lett, 21: 243–252. doi:10.1111/ele.12889

Tillman-Sutela, E., A. Kauppi, K. Karppinen, and D. F. Tomback. 2008. Variant maturity in seed structures of Pinus albicaulis (Engelm.) and Pinus sibirica (Du Tour): Key to a soil seed bank, unusual among conifers? Trees - Structure and Function 22:225–236.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird 16:123-161

Tomback, D. 1982. Dispersal of Whitebark Pine Seeds by Clark's Nutcracker: A Mutualism Hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D. F. 2005. The impact of seed dispersal by Clark's nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. Pages 181–201 *in*: G. Broll and B. Keplin, eds. Mountain ecosystems: studies in treeline ecology. Springer, New York.

Tomback, D. F., and P. Achuff. 2010. Blister rust and western forest biodiversity: Ecology, values and outlook for white pines. Forest Pathology 40:186–225.

Tomback, D. F., S. K. Sund, and L. A. Hoffmann. 1993. Postfire regeneration of pinus-albicaulis - height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research 23:113–119.

Tomback, D. F., S. F. Arno, and R. E. Keane, eds. 2001a. The compelling case for management intervention. Pages 3-25 *in*; Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Tomback, D. F., A. J. Anderies, K. S. Carsey, M. L. Powell, and S. Mellmann-Brown. 2001b. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology 82:2587–2600.

(USFS) United States Forest Service. 2015. The rising cost of wildfire operations: effects on the Forest Service's non-fire work. USDA Forest Service. available at:

https://www.fs.fed.us/sites/default/files/2015-Fire-Budget-Report.pdf

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20160373.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. Science 313:940–943.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences 108:13165–13170.

Zwolak, R., D. E. Pearson, Y. K. Ortega, and E. E. Crone 2010. Fire and mice: Seed predation moderates fire's influence on conifer recruitment. Ecology, 91: 1124–1131. doi:10.1890/09-0332.1