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Canopy structure and below-canopy temperatures interact to shape seedling response to disturbance in a Rocky Mountain subalpine forest

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ABSTRACT

We examined the effects of two recent, high-severity disturbances on seed dispersal and conifer seedling establishment in a subalpine spruce-fir forest in the San Juan Mountains, Colorado. Our study area had undergone high forest mortality from a spruce beetle (*Dendroctonus rufipennis*) outbreak beginning ca. 2004, and a portion of the study area was additionally burned by the West Fork Complex wildfire in 2013. The aim of this study was to determine how seedling re-establishment patterns vary with seed availability, temperature, overstory composition, and understory cover across a topographically heterogeneous landscape with varying disturbance impacts. We established thirty study sites in the burned area and sixty sites in the unburned, beetle-affected area in order to capture a gradient of beetle outbreak severity. We assessed post-disturbance regeneration by conducting seedling counts in the summer of 2018, five years after the fire and more than a decade since the onset of the beetle outbreak. We determined seedling establishment after disturbances by using terminal bud scar counts to estimate seedling age. We measured Engelmann spruce (*Picea engelmannii*) seed dispersal and below-canopy temperatures over three years (2017–2019) using *in situ* seed traps and Logtag® temperature sensors at 2 m height. We assessed relationships between (1) seed availability and live overstory remaining after the spruce beetle outbreak, and (2) seedling abundance and all explanatory variables using hierarchical Bayesian models. Conifer seed and seedling counts were zero in most of the burned area, though there was abundant aspen regeneration at lower elevations. In unburned, beetle-affected forests, we found that the degree of spruce overstory mortality did not strongly affect seed availability but showed a strong effect on spruce seedling densities. Conifer seedling densities were also influenced by below-canopy temperatures, aspect, and understory litter and shrub cover. These results indicate that the West Fork Complex fire has potentially resulted in a long-term loss of conifer forest throughout much of the burn area where distance to a seed source is > 100 m. High-severity spruce beetle outbreaks have also limited regeneration, although seedlings are still present in the majority of beetle-killed sites. Future patterns of re-establishment will also be strongly influenced by topography and future warming trends.

1. Introduction

Forest ecosystems of western North America have experienced bark beetle outbreaks and wildfires, among other disturbances, for millennia. However, climate change creates uncertainty around how forests will recover from these disturbances, and whether extensive mortality may lead to ecosystem conversions (IPCC, 2014). Evidence from around the globe suggests that forest disturbance frequency, severity, and extent are increasing as a result of warming temperatures, and that these changing disturbance regimes may exceed species' recovery mechanisms (Allen et al., 2010; Seidl et al., 2017). Furthermore, warming temperatures and drought stress may create unsuitable conditions for re-establishment of tree species that originally established under cooler climates decades or centuries ago (Johnstone et al., 2016).

For the past two decades, increasingly hot and dry conditions have caused extensive bark beetle outbreaks and wildfire activity in the southern Rocky Mountains (Bentz et al., 2010; Rocca et al., 2014). Bark beetles have caused tens of millions of hectares of conifer mortality across western North America, while annual area burned in the southern Rockies has more than tripled since the 1970's (Westerling, 2016). Recent studies documented declines in seedling recruitment following forest fires in the Rockies which have been attributed to

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warm, dry post-fire conditions (Harvey et al., 2016; Rother and Veblen, 2016; Savage et al., 2013; Stevens-Rumann et al., 2018). Increasing fire size and severity may also contribute to reduced establishment, as non-serotinous species such as Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are not able to disperse large distances into the interiors of burned patches with no available seed sources (Harvey et al., 2016; Turner et al., 1999; Urza and Sibold, 2017). Impacts of bark beetle outbreaks on seedling recruitment have not been as widely documented, but there is evidence that higher-severity outbreaks may limit recruitment of shade-tolerant species (Pelz et al., 2018).

There are several mechanisms by which increasing disturbance severity (i.e., greater losses of living vegetation and greater impacts to soils) may reduce species' resilience (Holling, 1973). In addition to reducing seed source availability within burn patches, severe wildfires may alter soil chemistry, lead to severe erosion, and elevate ground-surface temperatures (Carlson et al., 2017; Certini, 2005; Carlson et al., in preparation). In contrast to fires bark beetle outbreaks typically do not affect the canopy as severely and do not disturb the soil surface, but may impact seedling regeneration by selectively killing large, seed-producing trees (Schmid and Frye, 1977). Canopy mortality additionally alters microclimate, light environments, and soil moisture on the ground surface, and may increase seedling exposure to warming temperatures (Davis et al., 2019b; Dobrowski et al., 2015; Edburg et al., 2012). However, canopy disturbance can also promote regeneration with suitable temperature and moisture conditions and sufficient seed supply. Fires expose mineral soils and provide opportunities for seedling establishment (Johnstone and Chapin, 2006), while bark beetle outbreaks may release the growth of understory saplings as a result of canopy opening (Veblen et al., 1991; Hawkins et al., 2013). Treefall following overstory die-off can additionally create favorable microhabitats for seedling establishment, as downed logs shade the soil and help to retain moisture (Jonášová and Prach, 2004).

Because subalpine forest species are slow-growing, and seedlings are more vulnerable to climate than adult trees (Dobrowski et al., 2015), post-disturbance establishment successes and failures will have long-term effects on the future trajectories of forests (Bell et al., 2014; Perovich and Sibold, 2016). Patches of overstory mortality with varying severity may result in differing patterns of seedling establishment, which may complicate how forests respond to warming temperatures at a landscape scale (Redmond and Kelsey, 2018; Turner, 2010). Understanding how forests are currently regenerating following severe overstory mortality events in the Rocky Mountains will therefore improve understanding of how disturbances and warming trends may interact to shape future forest development (Johnstone et al., 2016).

Disturbances may make high-elevation Rocky Mountain forest species more vulnerable to climatic stress (Dobrowski et al., 2015). Dominant spruce and fir species are shade-tolerant and will not necessarily benefit from increased light availability following canopy removal (Knapp and Smith, 1982). Seedling germination and survival also depends on adequate soil moisture and snowpack (Andrus et al., 2018), which may be reduced by disturbance (Pugh and Small, 2013). However, longer snow-free periods may increase annual growth in established seedlings (Hill et al., 2019). Canopy loss from bark beetle outbreaks may additionally result in cooling of overnight temperatures, mitigating the effects of warming on soil moisture and snowpack losses (Carlson et al., in preparation). Furthermore, impacts of disturbance on below-canopy climates may be highly variable in topographically complex mountain regions like the southern Rockies. Topographic features such as north-facing slopes, high elevations, and cold-air drainages may allow sites to remain sufficiently cool and moist to continue supporting cold-adapted spruce and fir regardless of disturbance impacts, while topographic settings supporting warmer and drier conditions (i.e. south-facing, low-elevation sites with high topographic relief) may be more vulnerable to disturbance-related transitions (Dobrowski, 2011).

The aims of this study were to determine how recent, severe bark beetle outbreaks and wildfire in the San Juan Mountains of southwest Colorado have affected (1) patterns of seed dispersal by *P. engelmannii* (hereafter referred to as 'PIEN'), and (2) conifer seedling establishment in relation to temperatures, understory composition, and seed availability. This region has undergone significant warming and multiple droughts since 2000, and mean annual temperatures have increased by ~2.0 °C from 1979 to 2019 (GridMET climate data, http://climateengine.org/). The spruce-fir forest in our study area has also undergone a severe spruce beetle (*Dendroctonus rufipennis*) outbreak beginning ca. 2004, and > 44,500 ha of beetle-affected forest were additionally burned by the West Fork Complex wildfire in 2013. We used hierarchical Bayesian models to assess the effects of each disturbance (spruce beetle outbreak and fire) on seed dispersal using three years of seed counts, and to assess the impacts of disturbance-caused canopy change and seed dispersal on conifer seedling abundance. Our models also included growing-season temperature averages recorded by *in situ* temperature sensors at 2 m height. While previous work has assessed the role of climate conditions in mediating post-disturbance recovery, few studies have investigated how recovery may be influenced simultaneously by temperature conditions in the below-canopy environment and by disturbance impacts on seed dispersal mechanisms.

2. Methods

2.1. Study area

Field sampling was located within a ~625 km^2 area around Wolf Creek Pass in the eastern San Juan Mountains (Fig. 1a). Terrain is steep and varied with elevations ranging from ~2700 to 3600 m. The forest is dominated by Engelmann spruce and subalpine fir. White fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), blue spruce (*Picea pungens*), and quaking aspen (*Populus tremuloides*) are also present. The high-elevation climate is characterized by mild summers, cold winters, and a short growing season. Most precipitation falls as winter snow (514 mm/year average) or rains brought by monsoonal storms in July-September (262 mm/year average). The area was burned by the West Fork Complex wildfire in 2013, a 44,515-ha event which burned at moderate to high severity (MTBS, 2013). Most of the unburned forest is in the early gray stage following spruce beetle outbreak, in which most killed trees have lost all needles but are still standing with fine twigs and branches remaining in the canopy. The outbreak, which is still ongoing, was first recorded in the study area in 2004 and is considered one of the highest-severity outbreaks occurring in North America in the last several decades (CSFS, 2018).

2.2. Field data

2.2.1. Site selection

We selected 60 sites in unburned forest and 30 sites in the West Fork Complex burn area to sample seedling abundance, overstory mortality, understory composition, seed dispersal, and below-canopy temperatures. Our final analyses used 58 unburned sites and 27 burned sites, as we were not able to successfully recover seeds in the seed traps from the remaining sites. Using GIS and aerial imagery, we selected sites that were accessible from roads and trails and that represented gradients in elevation, aspect, topographic position, and spruce beetle outbreak severity. More sites were placed in unburned forest in order to assess the effects of canopy cover gradients on temperature (Carlson et al., in preparation) and seed abundance. In the burned area, we selected sites at varying distances from unburned edges. We measured distance from each burned site to unburned forest edge in GIS by overlaying site GPS coordinates on a burn severity classification obtained from the Monitoring Trends in Burn Severity (MTBS) program (mtbs.gov; Fig. 1b).

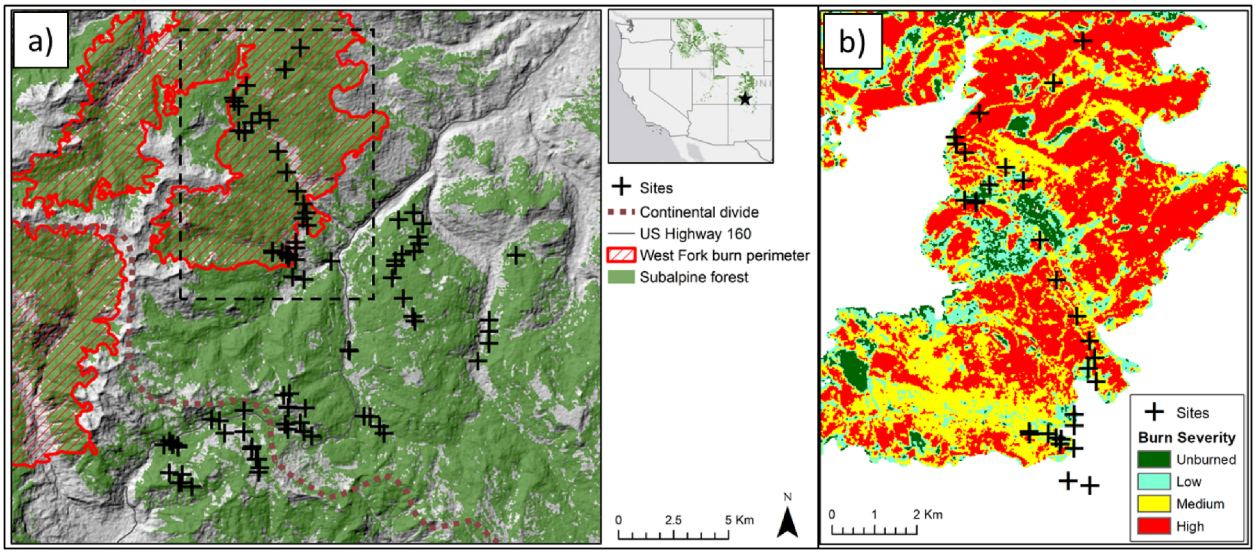

Fig. 1. (a) Map of study sites. Inset map shows the location of the study area within the western United States. Most forested area (in green) is affected by the spruce beetle outbreak to some degree. Dashed box indicates the area shown in figure (b). (b) Study sites in the burned area overlain on burn severity classes mapped by the Monitoring Trends in Burn Severity program (mtbs.gov). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2.2. Seed dispersal

We sampled seed abundance at each site using seed traps fixed to the ground. Seed traps were designed to capture wind-dispersed seed rain, which is the primary mechanism of seed dispersal in PIEN (Alexander, 1987). Traps were square baskets constructed from fine mesh, covered with hardware cloth with 0.64-cm openings to prevent seed predation by birds and small mammals (Fig. 2). Coverings were fastened to the ground with metal stakes. We initially placed the traps at each field site in early September 2016, before the period of peak seed dispersal for PIEN in late fall-early winter (Alexander, 1987). We collected seeds following snowmelt in June-July of 2017, 2018, and 2019. After separating PIEN seeds from litter and other material in the trap, we counted all wing structures with intact seeds attached. Because fir species have not undergone major disturbance in our study area, and because periods of peak dispersal differ between PIEN and fir species present in the study area, we did not assess patterns in fir seed abundance.

2.2.3. Temperature data

We sampled below-canopy temperatures at each site continuously throughout the snow-free season of 2017 (June-October) using Logtag®

Fig. 2. A seed trap.

temperature sensors. While temperatures for a single growing season may not represent the average conditions of the past several years of seedling recruitment, we assumed that temperature records reflect topographic influences on climate that remain consistent over time. Our goal was therefore not to determine absolute ideal temperatures for PIEN seedlings, but to determine the extent to which seedling abundances are influenced by these relative differences in temperature. We did not assess the effect of winter temperatures on seedling abundance for three reasons: first, temperature records during the winter of 2016–2017 were unusable at many sites due to influence of snow cover on the temperature sensors; second, temperatures during the winter of 2017–2018 were affected by an exceptionally low snowpack which may not be representative of the past decade in which our seedlings established; and third, summer and winter temperatures were strongly correlated for individual sites.

We placed sensors inside plastic radiation shields covered in reflective tape to prevent direct solar radiation. Sensors and radiation shields were attached to tree trunks ~2 m above the ground. We placed sensors at this height to minimize effects of snow insulation on temperature recordings, as patchy snow cover can persist well into the summer in this area. Sensors were programmed to record every three hours. From these recordings we derived daily maximum and minimum temperatures (Tmax and Tmin) and calculated the means of each of these values over the snow-free season for each site.

2.2.4. Overstory mortality and topographic characteristics

We assessed live canopy and overstory mortality at each unburned site within a 20 m × 20 m square plot area. While measurements of dead trees included non-beetle-caused mortality, most of the mortality in our plots could be attributed to beetle kill. Plots were measured from the tree where temperature sensors were fixed and extended 10 m in each of the four cardinal directions. We measured diameter at breast height (DBH) of all live and dead trees taller than breast height that were rooted within the plot. DBH measurements were summarized as total basal area for all live trees, live PIEN, live fir, live *P. tremuloides* (POTR), and dead PIEN for each plot. To characterize site topography, we measured aspect and slope at plot centers. We converted aspect to a relative northeast-to-southwest-facing scale using the equation $Taspect = \sin(aspect + 45) + 1$ (Beers et al., 1966).

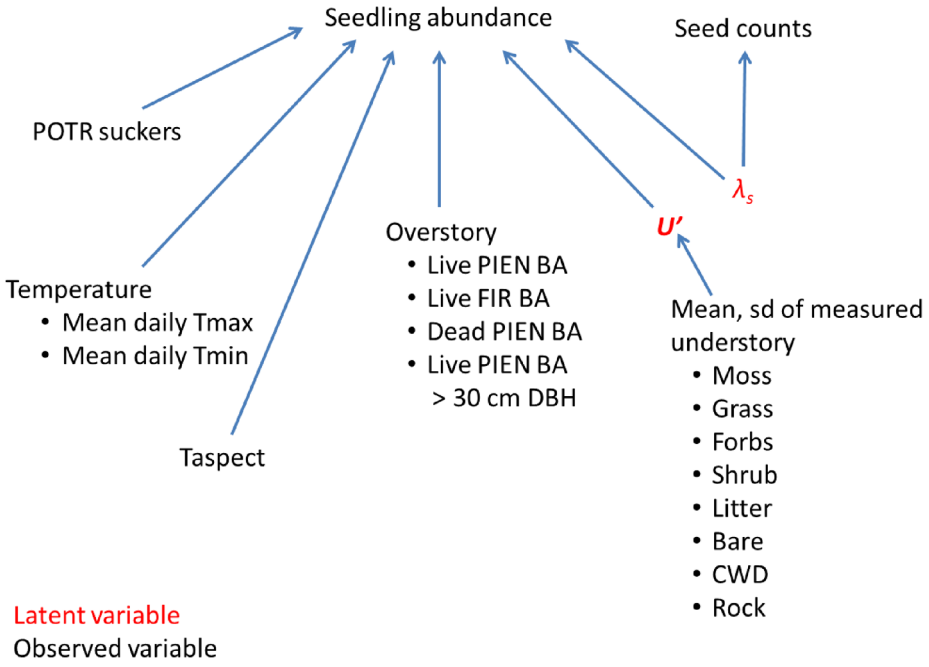

Fig. 3. Diagram of hypothesized relationships between measured variables and seedling counts. Latent variables (red) are treated as unobserved, random variables in hierarchical Bayesian models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2.5. Understory

We measured understory composition using fifteen 1 m × 1 m square subplots per plot. Subplots were placed at randomly selected intervals along the central north-south and east-west-running transects of the plot. We placed subplots using a PVC frame and visually estimated percent cover of each of eight understory classes: Moss, Grass, Forbs, Shrub, Litter, Bare, Coarse Woody Debris (CWD; defined as debris > 5 cm wide at the widest point), and Rock. Subplot percent cover estimates were then used to derive the mean and standard deviation of plot-level percent cover for each understory class.

2.2.6. Seedling counts

We conducted seedling counts for each site during August-September of 2018. We measured the same 20 m × 20 m plot areas used to measure overstory and counted all tree seedlings and saplings < 1 m in height for all species present. Counts included both conifer and POTR seedlings. We assessed seedling age for conifers by counting terminal bud scars associated with annual growth, which has been shown to be a reasonably accurate method for aging PIEN seedlings up to ~14 years old (Urza and Sibold, 2013). We counted seedlings estimated to be < 10 years old, assuming that these represented establishment that occurred after the onset of the spruce beetle outbreak.

2.3. Analysis

Due to low seed and seedling counts in the burned area, we statistically modeled abundances in unburned, beetle-killed sites only. We assessed effects of burn severity and distance to seed source on seed and seedling abundance in the burned area by mapping counts over MTBS burn severity classes and by visually assessing plots of seed/seedling abundance by distance to unburned pixels. For unburned sites, we used a Bayesian hierarchical modeling approach in order to account for uncertainty in understory cover from multiple sub-samples per plot, and seed abundances sampled in multiple years. All models were fit by Markov Chain Monte Carlo simulations with 10,000 iterations, implemented with the JAGS (Just Another Gibbs Sampler) algorithm in the 'rjags' package in R (Plummer, 2017, 2018; R Core Team, 2019).

2.3.1. Seed dispersal model

We used a hierarchical Bayesian model to assess the relationship between live PIEN basal area and seed abundance in unburned sites. For sites with live PIEN, we calculated the basal area of all live PIEN trees at least 30 cm in diameter (*LivePIENOver*30). Although Alexander (1987) reported that a diameter of 38 cm is required for PIEN trees to become significant seed producers, there were only two sites with live trees of that diameter. Expected annual seed abundance at each site j was treated as a latent variable, $\lambda_{s,j}$, from which observed seed counts in 2017, 2018, and 2019 were drawn. Probabilities of observed seed counts for each site and year i (s_{ij}) were modeled as a Poisson distribution with median $\lambda_{s,j}$. $\lambda_{s,j}$is drawn from a gamma distribution predicted with the equations

$$\lambda_{s,j} \sim \text{gamma}\left(\frac{\mu_{s,j}^2}{\sigma_s^2}, \frac{\mu_{s,j}}{\sigma_s^2}\right)$$

$$\mu_{s,j} = \gamma_1 + \gamma_2(\mathit{LivePIENOver30}_j)$$

where γ_s's are unknown coefficients, $\mu_{s,j}$ is the mean of a gamma distribution predicting $\lambda_{s,j}$, and σ_s^2 is the unknown variance of the gamma distribution. μ_s and σ_s^2 were used to derive shape and rate parameters using moment-matching equations. γ's and σ_s^2 were assigned uninformative priors. The full posterior expression for the seed count model is

$$[\gamma_1, \gamma_2, \sigma_s^2|\boldsymbol{s}] \sim \prod_{i=1}^{3}\prod_{j=1}^{58} \text{Poisson}(s_{i,j}|\lambda_{s,j}) \times \text{gamma}(\lambda_{s,j}|\gamma_1, \gamma_2, \sigma_s^2, \mathit{LivePIENOver30}) \times \text{normal}(\gamma_1|0, 0.001) \times \text{normal}(\gamma_2|0, 0.001) \times \text{inverse gamma}(\sigma_s^2|0.001, 0.001)$$

2.3.2. Seedling abundance model

We used additional Bayesian models to determine how PIEN and fir seedling counts varied with site temperature, aspect, overstory composition, understory, and competition from POTR suckers in unburned sites (all potential relationships are diagrammed in Fig. 3; variable descriptions are given in Table 1). We fit models using both PIEN and fir seedlings < 10 years old as the response variable. For each site j,

Table 1
Candidate variables for Bayesian seedling abundance models.

Variable	Description
Tmax	Mean growing-season daily maximum temperature
$Tmax^2$	Quadratic form of Tmax
Tmin	Mean growing-season daily minimum temperature
$Tmin^2$	Quadratic form of Tmin
Taspect	Transformed aspect measured at plot center (Beers et al., 1966)
Slope	Slope measured at plot center
LivePIEN	Basal area of live spruce trees > 5 cm in diameter
LiveFIR	Basal area of live fir trees (subalpine and white fir) > 5 cm in diameter
LivePIENOver30	Basal area of live spruce trees > 30 cm in diameter
POTR	Count of aspen seedlings < 1 m in height
Moss	Percent cover of each understory category (drawn from beta distributions defined by observed means and standard deviations from 15 subplots)
Grass	
Forb	
Shrub	
Litter	
CWD	
Rock	
Bare	
Seed count (λ_s)	PIEN seed count (PIEN models only; mean of Poisson distribution for observed values)

seedling count (y_j) was modeled as a sample drawn from a Poisson distribution with mean λ_j predicted by a linear combination of site variables (temperature, topography, and overstory; assumed to be measured without error), and hierarchical understory and seed count variables. The model is described by the equations

$$y_j \sim Poisson(\lambda_j)$$

$$\lambda_j = \exp(\beta_0 + \boldsymbol{\beta X}_j^{'} + \boldsymbol{\beta}_U \boldsymbol{U}_j^{'} + \beta_s \lambda_{s,j})$$

where $\boldsymbol{X}$ is a matrix of predictor variables (those assumed to be measured without error), $\boldsymbol{U}$ is a matrix of latent understory cover values constrained by means and standard deviations of subplots, $\lambda_{s,j}$ is a latent variable representing annual mean seed count, and $\boldsymbol{\beta}$, $\boldsymbol{\beta}_U$ and β_s are coefficients. In these models, expected seed count (λ_s) was assigned an uninformative prior rather than being predicted by *LivePIENOver30*. This was because a term for live PIEN overstory was already included in $\boldsymbol{X}$ as a direct effect on seedling abundance. The full posterior expression for the seedling abundance model is

$$[\beta_0, \boldsymbol{\beta}_X, \boldsymbol{\beta}_U, \beta_s, \boldsymbol{\lambda}_s, \boldsymbol{U} | \boldsymbol{y}, \boldsymbol{s}] \sim \prod_{i=1}^{3} \prod_{j=1}^{58} \text{Poisson}(y_j | \beta_0, \boldsymbol{\beta}_U, \boldsymbol{U}_j^{'}, \boldsymbol{\beta}_s, \lambda_{s,j}, \boldsymbol{\beta}_X, \boldsymbol{X}_j^{'})$$
$$\times \text{Poisson}(s_{i,j} | \lambda_{s,j}) \text{gamma}(\lambda_{s,j} | 0.001, 0.001)$$
$$\times \prod_{k=1}^{p_U} \text{beta}(\boldsymbol{U}_{j,k} | m_{j,k}, sd_{j,k}) \text{normal}(\beta_{U,k} | 0, 0.001)$$
$$\times \prod_{l=1}^{p_X} \text{normal}(\beta_{X,l} | 0, 0.001) \times \text{normal}(\beta_s | 0, 0.001)$$
$$\times \text{normal}(\beta_0 | 0. , 0.001)$$

where $m_{j,k}$, $sd_{j,k}$ are the observed mean and standard deviation of 15 understory subplots at site j for understory category k, and are used for deriving shape and range parameters for the beta distribution using moment-matching equations. β values were assigned uninformative normal priors.

2.3.3. Indicator variable selection

Due to the large number of predictor variables in the seedling abundance model (Table 1), we selected a parsimonious model using an indicator variable selection procedure (George and McCulloch, 1993). This involved adding a vector of binary indicator variable terms, $\boldsymbol{z}$, to the model such that each variable n in the linear regression model is multiplied by $z_n * \beta_n$. The model was then fit using MCMC sampling, with each iteration assigning a value of 0 or 1 to z's to effectively include or exclude variables from the model. The posterior means of z's indicate overall variable importance (means closer to 0 mean variables are unimportant, means closer to 1 indicate greater importance). We assigned priors to z's and β's with the 'slab-and-spike' method described by Kuo and Mallick (1998), which uses independent distributions for both variables. The prior distribution for each z_m term was

$$z_m \sim \text{Bernoulli}(\rho)$$

where ρ was constrained by an informative beta prior resulting in a most likely value of 0.5. The prior distribution for each β_m was

$$\beta_m \sim \text{normal}(0, \tau)$$

where τ was assigned an uninformative inverse gamma prior. The full model expression with indicator variables included is

$$[\beta_0, \boldsymbol{\beta}_X, \boldsymbol{\beta}_U, \beta_s, \boldsymbol{\lambda}_s, \boldsymbol{U}, \boldsymbol{z}, \rho, \tau | \boldsymbol{y}, \boldsymbol{s}] \sim \prod_{i=1}^{2} \prod_{j=1}^{58} \text{Poisson}$$
$$(y_j | \beta_0, \boldsymbol{\beta}_U, \boldsymbol{z}_U, \boldsymbol{U}_j^{'}, \beta_s, z_s, \lambda_{s,j}, \boldsymbol{\beta}_X, \boldsymbol{z}_X, \boldsymbol{X}_j^{'})$$
$$\times \text{Poisson}(s_{i,j} | \lambda_{s,j}) \text{gamma}(\lambda_{s,j} | 0.001, 0.001) \times \prod_{k=1}^{p_U} \text{beta}(\boldsymbol{U}_{j,k} | m_{j,k}, sd_{j,k})$$
$$\times \text{normal}(\beta_{U,k} | 0, \tau) \text{Bernoulli}(z_{U,k} | \rho)$$
$$\times \prod_{l=1}^{p_X} \text{normal}(\beta_{X,l} | 0, \tau) \text{Bernoulli}(z_{X,l} | \rho)$$
$$\times \text{normal}(\beta_s | 0, \tau) \text{Bernoulli}(z_s | \rho) \times \text{beta}(\rho | 5, 5)$$
$$\times \text{inverse gamma}(\tau | 0.001, 0.001) \times \text{normal}(\beta_0 | 0, 0.001)$$

We used the posterior means of z's to determine variable subsets to include in final models, using a threshold of 0.5. We then fit final models without indicators to find posterior distributions for β's.

3. Results

3.1. Seed dispersal

We collected seeds from 27 of the 30 burned sites and 58 of the 60 unburned sites in at least one year. We were unable to obtain seed counts at the remaining sites due to lost traps or trap covers becoming separated. The number of sites where we obtained reliable seed counts in each year is as follows: 2017 – 26 burned, 50 unburned; 2018 – 22 burned, 54 unburned; 2019 – 22 burned, 50 unburned.

In the burned area, only six sites had non-zero PIEN seed counts in all three years (average per-year counts of 0.33–1.0 seeds). All sites where seeds were present are located less than 100 m from unburned edges (Fig. 4). The maximum seed count for a single year was 3. We did not find seeds from any other conifer species in our seed traps in burned sites.

Mean seed count in unburned sites was 7.0 seeds per year (std. dev. = 12.7), with a maximum of 117 seeds collected in one year at a single site. Four unburned sites had total seed counts of 0 for all three collection years. The Bayesian regression model for unburned sites indicated that there is a slight positive relationship between expected mean seed count (λ_s) and site-level basal area of PIEN > 30 cm in diameter, with a 79% probability that the regression coefficient (γ_2) is greater than 0 (95% credible interval = −0.12 to 0.19; Fig. 5).

3.2. Seedling abundance

In the burned area, only three sites contained conifer seedlings that had established in the five years since the fire. Each of these sites was located < 100 m from unburned forest near the edge of the burn perimeter (Fig. 6). These sites had also burned at low severity and contained seedlings older than five years which had survived the fire. Only one site with PIEN seedlings contained a single potentially viable

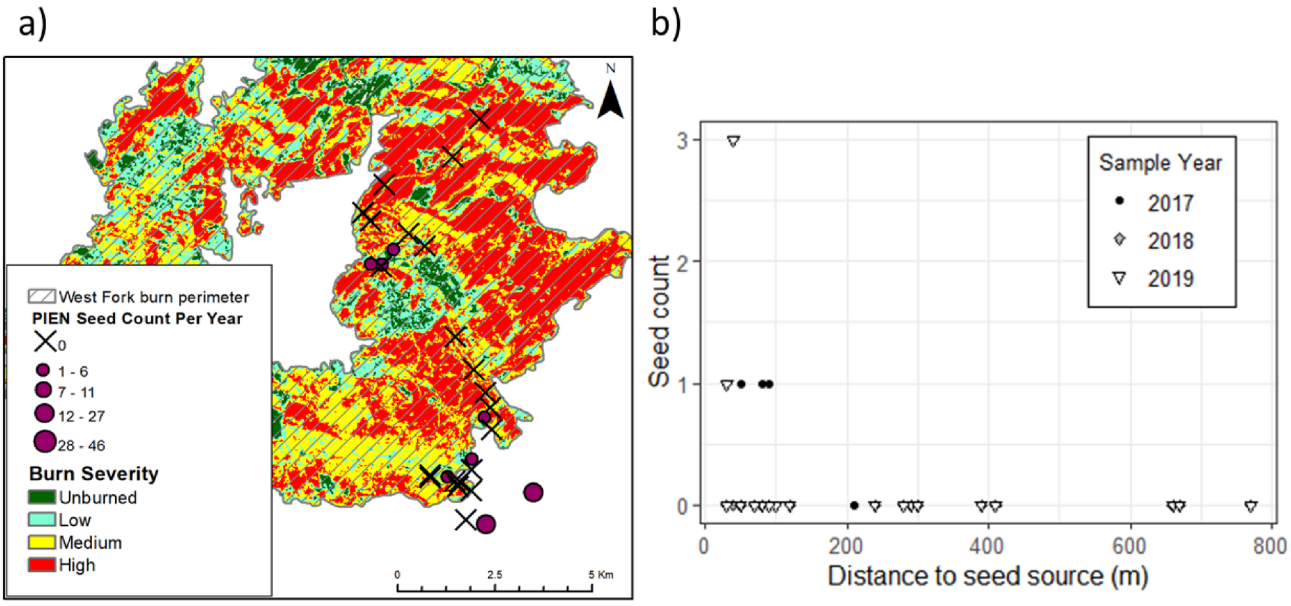

Fig. 4. (a) Map of seed counts for sampled sites in the West Fork Complex burn area, overlain with burn severity classes from MTBS. (b) Plot of seed counts in burned sites by distance to seed source, for all three collection years.

seed in the seed trap counted in one collection year, while the other two sites had seed counts of zero in all three years. In contrast to the low rates of conifer regeneration, many burned sites contained abundant POTR regeneration (mean density: 788.81 ± 1460.5 suckers/ha). POTR suckers were only present at sites below 3341 m in elevation (Fig. 7).

Seedling abundance was highly variable in unburned sites. The average density of sampled PIEN seedlings < 10 years old was 250.0 ± 420.7 seedlings/ha (mean ± one std. deviation) and the average density of PIEN seedlings 10 years or older was 252.2 ± 234.4 seedlings/ha. Ten sites contained no PIEN seedlings < 10 years old, although PIEN seedlings/saplings ≥10 years old were present at all sites. The average density of fir seedlings < 10 years old was 278.0 ± 427.6 seedlings/ha, and the density of fir seedlings ≥10 years old was 289.7 ± 344.8 seedlings/ha. Very few seedlings had established in the last three years (mean densities: 20.7 ± 57.6 seedlings/ha for PIEN, 19.0 ± 57.3 seedlings/ha for fir). Temporal patterns in seedling establishment were similar for PIEN and fir, with a majority of seedlings ≥10 years old (Fig. 8). Low abundances of seedlings established in 2016–2018 correspond with severe drought in 2018 as measured by the Palmer Drought Severity Index (PDSI; data from climateengine.org/). However, low PDSI values in 2012–2013 do not appear to affect seedling abundances.

The indicator variable selection procedure for PIEN models resulted in a final model that included Tmax, Tmin, Taspect, DeadPIEN, LiveFIR, Shrub, Litter, and CWD (Table 2). Seed count was not included. Although only the quadratic forms of Tmax and Tmin had mean z's > 0.5, we retained both the linear and quadratic forms of both variables. For fir *spp.* models, indicator variable selection resulted in a final model that included LiveFIR, POTR seedling count, and understory percent cover of Moss, Litter, CWD, and Bare. Temperature variables, Taspect, DeadPIEN, and understory percent cover of Grass, Forb, and Shrub were not included in fir seedling models. Slope and LivePIEN were not included in either PIEN or fir *spp.* models.

Variables in the final PIEN seedling abundance model with a > 95% probability of being non-zero (strong predictors of seedling abundance) include Taspect, DeadPIEN, LiveFIR, Tmax, Tmax^2, Tmin, Tmin^2, Shrub, and Litter (Table 3). PIEN seedling abundance is positively

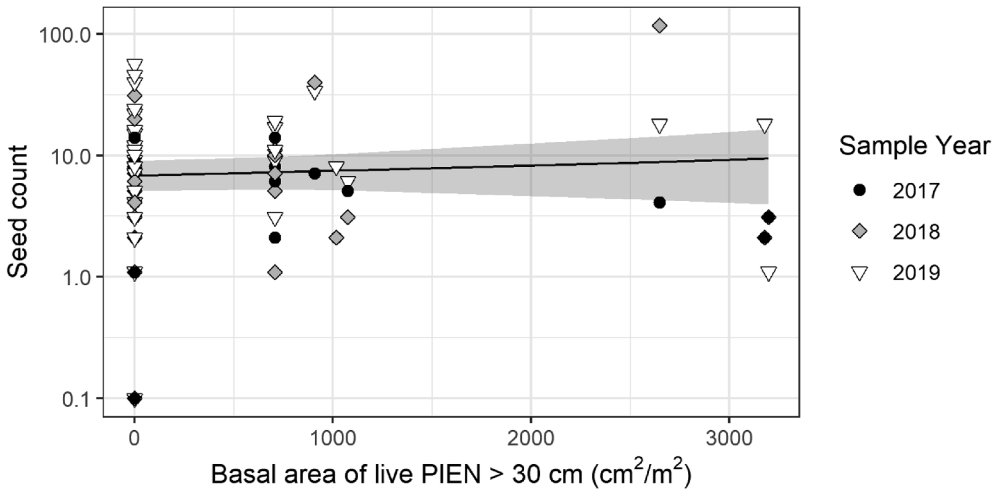

Fig. 5. Modeled relationship between expected seed counts (s) and basal area of live PIEN > 30 cm in diameter in unburned, beetle-affected forest. Black line: means of posterior distributions for predicted seed counts (μ_s); gray shaded area: 2.5th-97.5th percentile ranges. Points depict observed seed counts for three sample years. Note that y-axis is on a log scale.

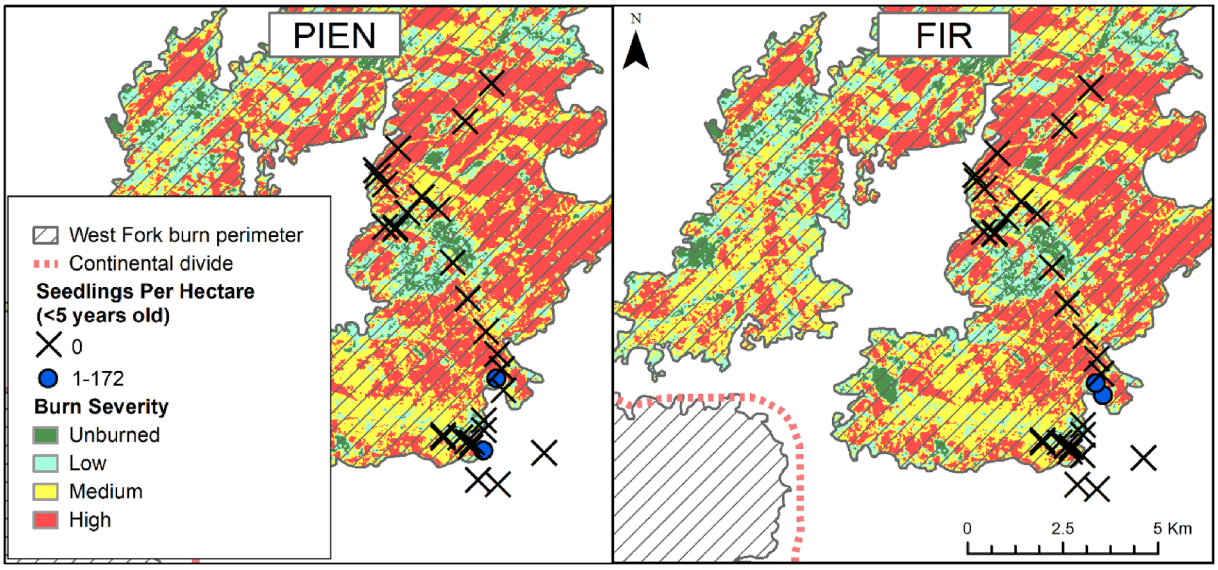

Fig. 6. Map of seedlings in the West Fork Complex burn area that established since the year of the fire (2013), with burn severity classes from MTBS.

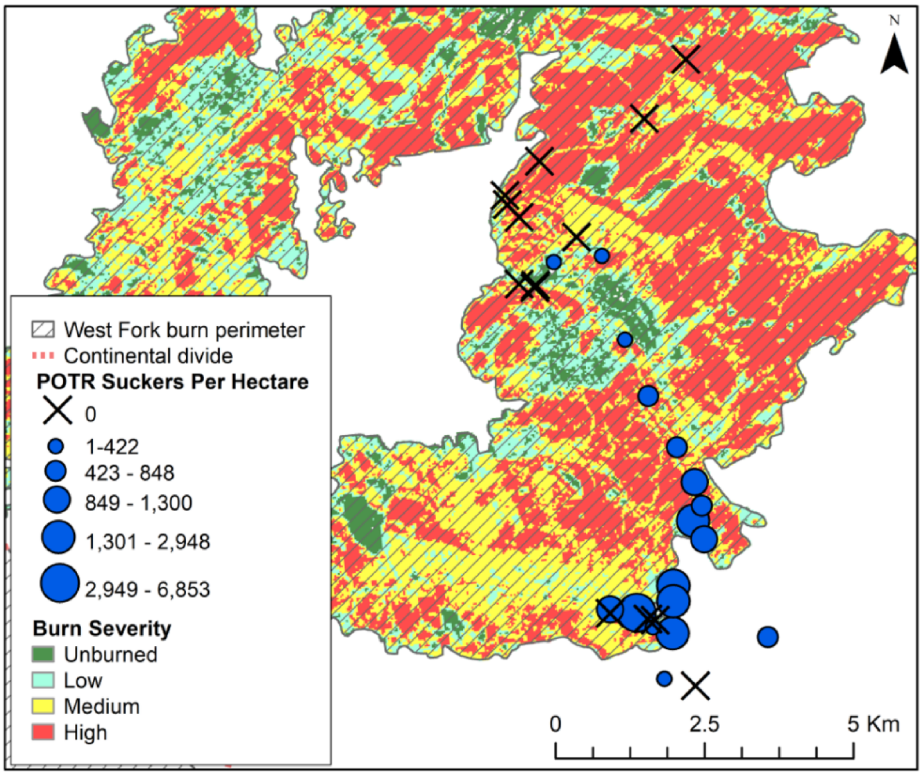

Fig. 7. Map of POTR suckers in the West Fork Complex burn area, with burn severity classes from MTBS.

correlated with increasing Taspect (i.e., more north-facing aspects), negatively correlated with increasing basal area of DeadPIEN, negatively correlated with increasing Shrub and Litter cover, and positively correlated with increasing Bare and Grass cover (Table 3; Fig. 9). Seedling abundance also decreases at the high ends of temperature ranges for both Tmax and Tmin, and mean response to Tmin indicates an optimal temperature at the colder end of the sampled range (~2 °C). Variables with a > 95% probability of being non-zero in fir *spp.* models include LiveFIR, POTR, CWD, and Bare (Table 3). Fir seedling abundance is positively correlated with increasing LiveFIR overstory basal area and with increasing POTR seedling abundance, and negatively correlated with increasing CWD and Bare percent cover (Table 3; Fig. 10).

4. Discussion

4.1. Patterns of regeneration in the West Fork burn area

We did not observe any conifer regeneration in severely burned areas of the West Fork Complex burn area five years after the fire. Conifer regeneration appeared to be constrained by a lack of available seed sources, as seedling absence corresponded with an absence of seed captured in seed traps. Given that most of the forested area burned at medium or high severity (Fig. 1b; MTBS, 2013), we may expect to see

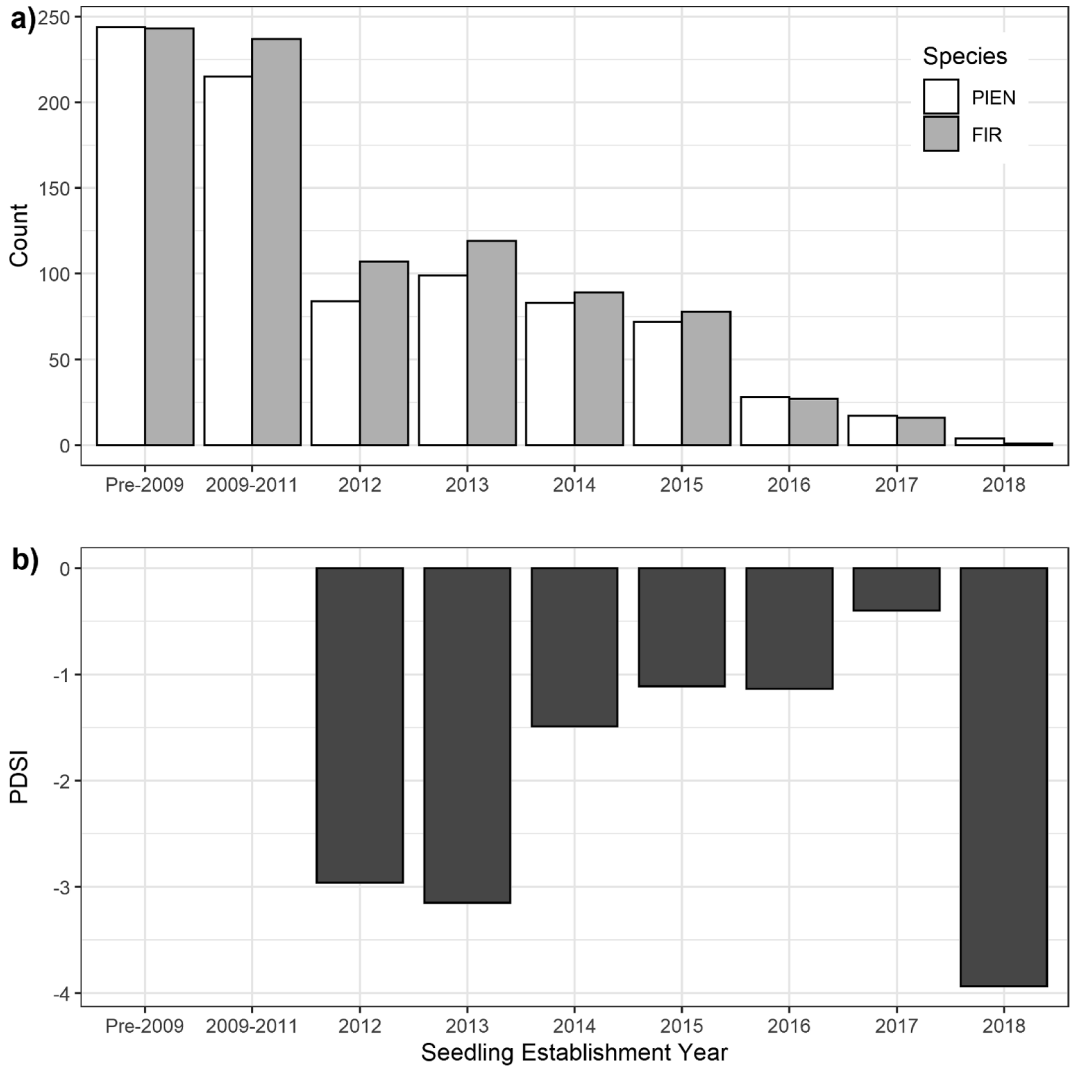

Fig. 8. (a) PIEN and fir *spp*. seedling counts by year of establishment for seedlings up to 10 years old in all unburned plots. Individual establishment years were determined up to 6 years prior to bud scar dating in 2018; older seedlings were classified as 7–10 years old or ≥10 years old. (b) Average PDSI for the study area by year (PRISM climate data; climateengine.org).

these patterns of extremely low conifer regeneration throughout the interior of the burned area. Regeneration of seed sources may take many decades as seeds establish within ~100 m of live forest edges, mature, and disperse seeds farther into the interior of the burn area. Current regeneration patterns suggest that lower elevations of the burn area will remain aspen-dominated for the next several decades or longer while higher elevations with no aspen regeneration may remain unforested meadows.

Seed dispersal limitations are evident, as 23 of 27 seed traps in the burned area (~85%) contained no conifer seeds in any collection year. Seeds were only present in low numbers in traps located within 100 m of the burn edge. This pattern was not unexpected given that Engelmann spruce and subalpine fir typically re-colonize burned areas by wind-dispersed seeds which do not typically travel farther than 100 m (Alexander, 1987). Although our seed trap design does not fully capture rare, long-distance seed dispersal events across the landscape (Nathan and Muller-Landau, 2000), the lack of seedlings at 93% of sites within the burned area suggests that these events are not leading to conifer re-establishment. Furthermore, regeneration has apparently not resulted from the pre-fire canopy seed bank. This can be an important seed source for post-fire regeneration in Engelmann spruce forests when seed production is abundant (Pounden et al., 2014). In the West Fork Complex, it is very likely that pre-fire cone production was diminished by the severe spruce beetle outbreak which killed most large-diameter spruce trees in the previous decade (Carlson et al., 2017).

Declining conifer regeneration following wildfire is an emerging pattern across the western United States as a result of increasing post-fire drought stress and low seed availability due to increasing fire sizes (Stevens-Rumann and Morgan, 2019). These regeneration failures may indicate that fires are catalyzing climate-driven ecosystem transitions (Davis et al., 2019a; Johnstone et al., 2016). Our results provide an additional example of potential post-fire regeneration failure in a high-elevation forest type, given that we only observed seedling establishment within close proximity of unburned edges. We can attribute this apparent forest transition to lack of seed dispersal, although the absence of seeds in most of our study sites obscures the potential concurrent role of warming and drought in limiting seedling establishment (Harvey et al., 2016; Kemp et al., 2019; Urza and Sibold, 2017).

Although droughts were not severe in the four years following the fire (Fig. 8), mean annual temperatures at Wolf Creek Pass have warmed by > 1.0 °C since 1990 (Rangwala and Miller, 2010). Carlson et al. (in preparation) found that mean temperatures in the burned area are elevated by ~0.5 °C compared to unburned areas with similar topographic characteristics. This temperature difference was observed at 2-m height and is likely to be even greater near the ground surface (Davis et al., 2019b). Re-establishing seedlings may therefore be

Table 2
Posterior means of indicator variables (z's) for all explanatory variables in models predicting seedling abundances for both *P. engelmannii* (PIEN) and fir *spp*. Values in bold are above the threshold of 0.5, and corresponding variables were included in final models. The full quadratic expressions of temperature variables were included. PIEN seed count was not considered in fir *spp*. models.

Variable	z– PIEN model	z– fir *spp*. model
Intercept	**1.00**	**0.97**
Tmax	**0.51**	0.44
$Tmax^2$	**0.51**	0.44
Tmin	**0.52**	0.39
$Tmin^2$	**0.50**	0.44
Taspect	**0.68**	0.30
Slope	0.34	0.41
LivePIEN	0.29	0.34
DeadPIEN	**0.91**	0.28
LiveFIR	**0.92**	**0.99**
POTR	0.28	**0.69**
Moss	0.44	**0.90**
Grass	0.41	0.40
Forb	0.46	0.48
Shrub	**0.84**	0.41
Litter	**0.99**	**0.67**
CWD	**0.53**	**0.99**
Rock	0.33	0.45
Bare	0.47	**0.77**
PIEN seed count (*s*)	0.47	–

Table 3
Variables in PIEN and fir *spp*. seedling abundance models and probabilities that β's are greater or less than 0. (+) indicates that $\beta_{mean} > 0$; (−) indicates that $\beta_{mean} < 0$. Values above 0.95 are in bold, indicating a > 95% probability that $\beta \neq 0$.

PIEN Model		Fir *spp*. Model	
Variable	Pr($\beta \neq 0$)	Variable	Pr($\beta \neq 0$)
Taspect	**0.98 (+)**	LiveFIR	**> 0.99 (+)**
DeadPIEN	**> 0.99 (-)**	POTR	**0.99 (+)**
LiveFIR	**> 0.99 (+)**	Moss	**0.99** (+)
Tmax	**> 0.99 (+)**	Litter	0.86 (+)
$Tmax^2$	**> 0.99 (−)**	CWD	**> 0.99 (−)**
Tmin	**> 0.99 (+)**	Bare	**> 0.99 (−)**
$Tmin^2$	**> 0.99 (−)**		
Shrub	**> 0.99 (−)**		
Litter	**> 0.99 (−)**		
CWD	0.82 (−)		

experiencing temperatures significantly warmer than those experienced when the pre-fire forest established. Greenhouse experiments have shown that Engelmann spruce seedling establishment, growth, and survival is sensitive to temperatures, with optimal growth occurring at daytime soil temperatures ~23 °C (Alexander, 1987). Furthermore, low soil moisture availability resulting from high temperatures and increased evaporative demand can severely limit seedling recruitment (Conlisk et al., 2017).

4.2. Patterns of regeneration in spruce beetle-killed forest

While seedling abundance was variable across the unburned, beetle-affected forest, we observed fairly high rates of post-disturbance seedling establishment at many of our study sites. There is abundant advance regeneration in the sub-canopy by both PIEN and fir saplings ≥10 years old at sites with both high and low levels of overstory PIEN mortality. Low abundances of seedlings and saplings < 10 years old, which are assumed to have established after the beetle outbreak, are typical for severely beetle-killed spruce-fir forests (Astrup et al., 2008; DeRose and Long, 2010). However, extremely low abundances of seedlings established in the last three years may indicate potential future trends that may arise from warming and severe droughts.

We observed a drop-off in seedling establishment from 2016 to 2018 which may be related to severe drought in 2018. While these drought conditions were not present in 2016–2017, the lagged effect might be due to mortality of newly established seedlings in fall 2017-summer 2018. We did not observe the same low seedling abundances in 2012–2013 despite low PDSI in those years. Both droughts were characterized by hot summers, low monsoon-season precipitation, and early snowmelt, while the drought of 2017–2018 also included very warm fall temperatures and extremely low winter snow cover. In addition to growing-season soil moisture, snowpack has been shown to strongly correlate with spruce and fir seedling establishment in both observational studies and growth experiments (Andrus et al., 2018; Kueppers et al., 2017). If warm fall-winter droughts such as the one in 2017–2018 are likely to occur more frequently in the San Juan Mountains in the near future, these events may limit future seedling establishment.

Bayesian analysis of site factors contributing to seedling abundance revealed that increasing temperatures may inhibit PIEN and fir *spp*. establishment, especially on drier, southwest-facing slopes. Our temperature data only represent a single growing season and therefore is not necessarily representative of absolute temperature-abundance relationships, but temperature patterns are reflective of relative spatial difference in temperatures which depend on topographic setting (Carlson et al., in preparation; Dobrowski, 2011). Our modeled temperature relationships therefore suggest that regional warming will cause PIEN and fir *spp*. seedling distributions to shift toward higher elevations, northeast-facing slopes, or valley bottoms with sufficient cold-air drainage to remain within their optimal temperature ranges. Due to differing responses to Tmax vs. Tmin, warming may be expected to affect PIEN distributions differently than fir *spp*. distributions and lead to shifts in species composition.

Seedling abundance models also revealed that the severity of spruce beetle mortality (as measured by basal area of standing dead PIEN) has strong effects on PIEN seedling establishment in relation to temperature and other site factors. A possible explanation for this relationship is that spruce beetle outbreak results in seed limitations as large-diameter, cone-producing trees die off. There is limited evidence for this mechanism from our seed dispersal model, but our variable selection procedure indicated that seed counts did not explain PIEN seedling abundance. It is possible that our analysis is limited by only having seed collections over three years, which may not fully capture year-to-year variability in seed production. Engelmann spruce produce bumper seed crops roughly every 2–5 years, and seed production is affected by multi-year weather conditions which impact various stages of seed development (Alexander, 1987; Buechling et al., 2016). Longer-term seed monitoring may be needed to more accurately assess effects of spruce beetle outbreak on overall seed supply.

Our results show that spruce seedling abundance is affected by live canopy cover, with seedlings responding positively to increasing overstory fir cover and negatively to increased spruce canopy loss. Although we did not see strong evidence that this is explained by seed dispersal, these relationships may be additionally influenced by changes in the below-canopy environment associated with live canopy. Dobrowski et al. (2015) observed that seedling densities increase with proportions of undisturbed forest cover across the western U.S., and hypothesize that this may be due to canopy cover buffering microclimates against broader warming trends. Spruce beetle outbreak does not lead to greater below-canopy warming, but may lead to greater overnight cooling (Carlson et al., in preparation) which may increase risk of frost damage at the onset of the growing season and potentially inhibit growth at cool edges of PIEN distribution (Hill et al., 2019; Noble and Alexander, 1977; Carlson et al., in review). Canopy loss may also lead to greater rates of snow ablation and earlier snowmelt (Pugh and Small, 2013). Furthermore, overstory die-offs may lead to declines in below-ground ectomycorrhizal associations, which has been shown to reduce seedling growth and survival in lodgepole pine stands

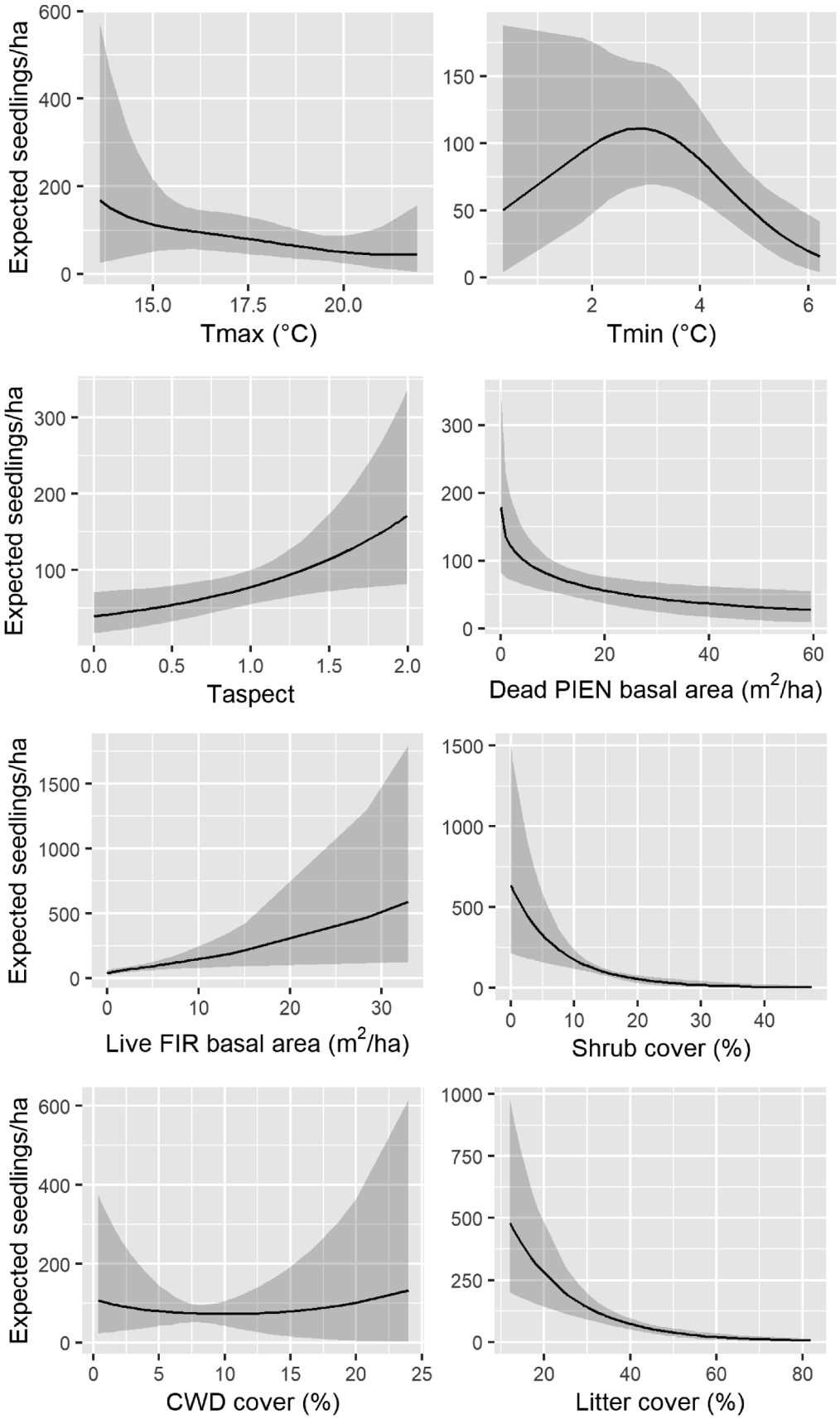

Fig. 9. Marginal response plots for all variables included in final PIEN seedling abundance models. Plots show the expected response of seedling abundance to each variable when all other variables are held at their mean values. Black lines show posterior means of predicted responses, gray shaded area shows the 95% credible interval.

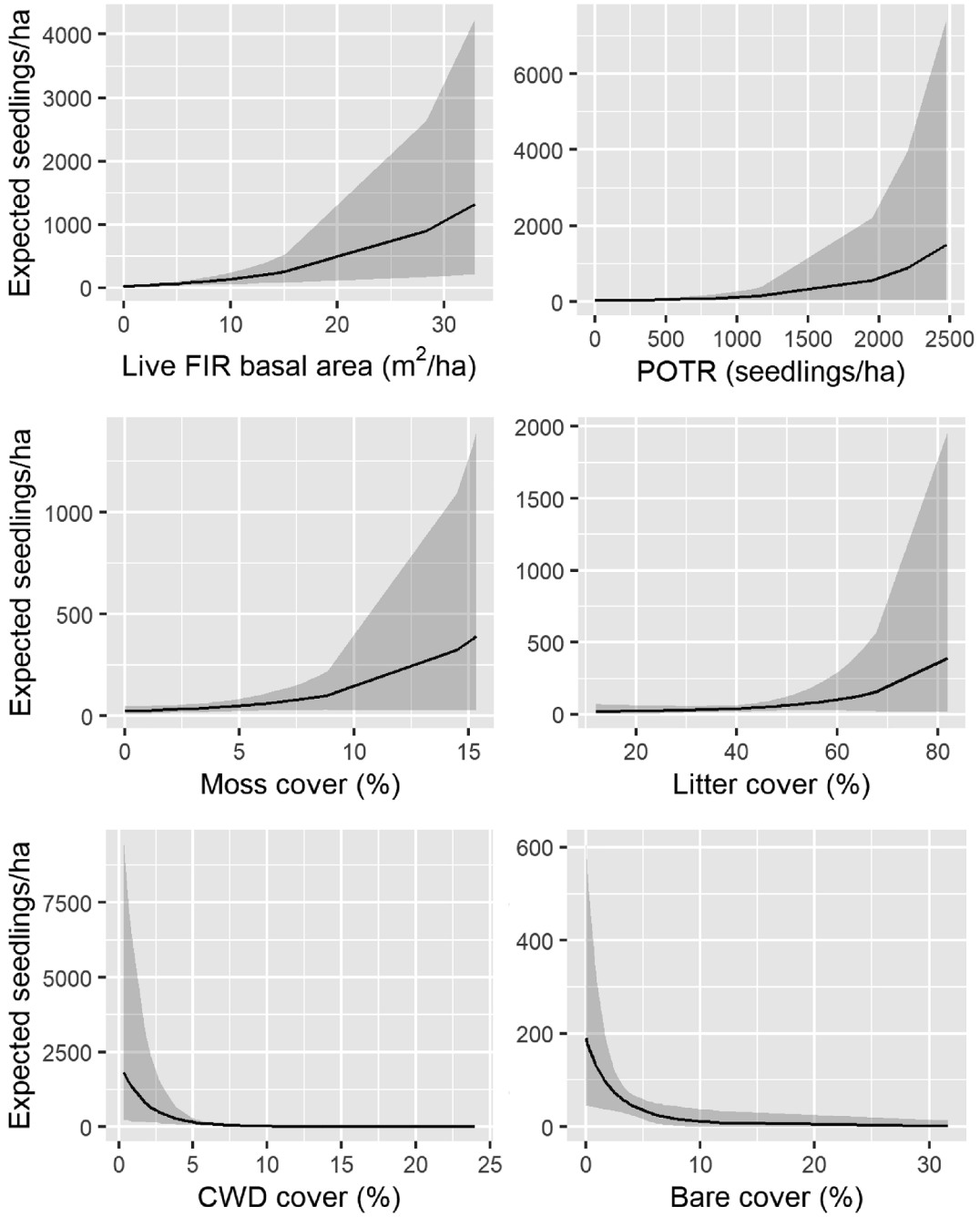

Fig. 10. Marginal response plots for all variables included in final fir *spp.* seedling abundance models. Plots show the expected response of seedling abundance to each variable when all other variables are held at their mean values. Black lines show posterior means of predicted responses, gray shaded area shows the 95% credible interval.

affected by mountain pine beetle (Karst et al., 2015). However, investigating this mechanism was beyond the scope of this study.

Finally, our analysis explored the role of understory composition in determining seedling abundance. We found that there were likely to be fewer PIEN seedlings at sites with greater litter and shrub cover, consistent with current understanding that PIEN prefers to establish on exposed mineral soil (Knapp and Smith, 1982; Noble and Alexander, 1977). Overstory mortality may be indirectly affecting PIEN regeneration by allowing for greater shrub growth as below-canopy light availability increases (Stone and Wolfe, 1996). Needle fall from the canopy may also initially increase understory litter cover following outbreak, creating a less favorable environment for PIEN seedling re-establishment. Furthermore, our results show that CWD did not favor seedling establishment for either PIEN or fir *spp*. and appeared to strongly inhibit fir establishment. It should be noted that most CWD we observed was from recent tree-fall as a result of the beetle outbreak. This relationship may change over time as logs decompose and form moist micro-sites for seedling establishment.

5. Conclusions

This study assessed patterns of seedling regeneration in forested area affected by a severe spruce beetle outbreak and a subsequent large, high-severity wildfire. Our results support two key conclusions: first, that conifer regeneration in the burned area is severely limited due to a lack of available seed sources; and second, that overstory mortality in

spruce beetle-killed forests is mediating the impacts of temperature and other site characteristics on seedling regeneration. The extremely low seedling abundances in sampled areas of the West Fork burn area fit in with a pattern being observed across the western United States, in which increasing fire sizes and severities in tandem with increasing post-fire aridity are reducing rates of forest regeneration. In beetle-killed forest, lower abundances of recently established PIEN seedlings in areas with greater overstory mortality has implications for long-term predictions of forest decline with climate change. While it is understood that temperature effects on seedling recruitment may vary at fine spatial scales in mountain forests, extensive canopy disturbances may also play an important role in accelerating forest decline.

CRediT authorship contribution statement

Amanda R. Carlson: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **JasonS. Sibold:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Visualization, Writing - review & editing. **José Negrón:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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