1 **TITLE: LIMITED CONIFER REGENERATION, BUT WIDESPREAD REGENERATION OF ASPEN SEEDLINGS**
2 **FOLLOWING THE CAMERON PEAK FIRE, NORTHWESTERN COLORADO**

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8 **ABSTRACT**

9 **Background**

10 Changing fire regimes and climate conditions have decreased postfire conifer regeneration densities in
11 many ecosystems across western North America. In the Southern Rocky Mountains, sparse postfire
12 regeneration of conifers has often been accompanied with abundant regeneration of quaking aspen,
13 much of which is from vegetative resprouting. While aspen also produce abundant lightweight seed that
14 can disperse great distances, we know considerably less about the patterns and drivers of postfire
15 establishment of aspen from seed. To understand the potential for severe fire to catalyze shifts to aspen
16 dominated forests, we studied recently burned conifer-dominated forests and asked (1) how does postfire
17 regeneration of conifers and aspen vary across sites? (2) how are aspen and conifer seedlings distributed
18 within sites? and (3) how do site and microsite conditions influence aspen seedling establishment? To
19 answer these questions, we conducted field surveys at 34 sites within the burn scar of the Cameron Peak
20 Fire, northwestern Colorado.

21 **Results**

22 Two years following fire, we found widespread but highly variable establishment of aspen seedlings,
23 despite the absence of aspen in the pre-fire stand. Aspen seedlings were more likely to occur at higher
24 elevations, where they were often clustered within concave microsites with bryophyte substrates and
25 near large coarse woody debris. Further we found aspen seedlings often outnumbered conifer seedlings
26 and occurred within the same local neighborhood as conifer seedlings.

27 **Conclusions**

28 Increased fire frequency, severity, and extent in western North America may exceed the capacity of
29 some formerly conifer-dominant forests to maintain historical distributions, while conditions following
30 high severity burns may allow establishment of aspen seedlings both within and outside of pre-fire aspen
31 populations.

32 **KEYWORDS**

33 aspen, postfire tree regeneration, seedling, *Populus tremuliodes,* sexual establishment

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BACKGROUND

Over the past two decades, fires have increased in frequency, size, and severity across the western United States (the West) (Parks and Abatzoglou 2020, Iglesias et al. 2022), largely due to climate warming (Abatzoglou and Williams 2016), more frequent human ignitions (Balch et al. 2017), and past land management practices (Allen et al. 2002). Not only is fire activity changing, numerous studies across the West have shown low postfire regeneration densities, and even complete regeneration failure, is becoming increasingly common (Stevens-Rumann and Morgan 2019, Coop et al. 2020). Low postfire regeneration has largely been attributed to more extreme fire behavior and severity. However, the effects of changing fire regimes and climate on postfire recovery are mediated by species-specific traits that drive seed production, germination, and seedling survival and growth, as well as biotic interactions in early seral communities (Lloret et al. 2005, Hansen et al. 2016, Davis et al. 2023). Understanding the complexity of these ecological relationships is not only a central challenge for fire ecology but also has huge implications for society.

There are three primary mechanisms that drive postfire tree regeneration: (1) vegetative resprouting, (2) germination of seed from live tree residuals or the unburned forest, or (3) germination of seeds from canopy seed banks. Because an individual's regeneration traits in part reflect the system's history of wildfire, alternations to fire regimes may compromise regeneration mechanisms that previously conferred resilience to wildfire (Johnstone et al. 2010). For example in lodgepole pine forests, short-intervals (i.e., <30 years) may lead to low post-fire regeneration when trees in the young pre-fire stand have not had enough time to develop serotinous cones (Turner et al. 2019). However, species rely upon multiple strategies may be more resilient to changing disturbance regimes. For example, quaking aspen (*Populus tremuloides*) may colonize burned areas through rapid suckering from root systems that survive fire or germination of seed from live trees (Baker 1925). Retaining both these strategies may allow quaking aspen to exist in a broader range of conditions and increase genetic diversity (Gill et al. 2017b, Landhäusser et al. 2019), thereby increasing its adaptive capacity to changing climate and disturbance regimes.

Concurrent with increases in fire frequency and severity, aspen is increasingly playing an important role in the post-fire ecology of many ecosystems across North America (Turner et al. 2003, Johnstone et al. 2010, Buma and Wessman 2011, Kulakowski et al. 2013, Gill et al. 2017b, Andrus et al. 2021, Kreider and Yocom 2021a, Nigro et al. 2022, Dawe et al. 2025). In the West most post-fire regeneration has historically been understood to be from root suckering, while in other parts of aspen's distribution seedling establishment is more widespread (Long and Mock 2012). These patterns have been hypothesized to occur as a result of differences in climate and the ensuing implications for trade-offs among growth, defense, and reproduction (Mock et al. 2012, DeRose et al. 2015, 2022). However, recent research suggests that post-fire aspen seedling establishment is more common across the West (Kreider and Yocom 2021a). Because aspen produce abundant lightweight seed that can be transported several kilometers by strong winds (Landhäusser et al. 2019), a greater role of seedling establishment profoundly increases the area across the West where aspen may establish following fire. This has important implications for post-fire ecosystem dynamics, particularly if aspen seedling establishment occurs in areas where conifer regeneration is limited (Andrus et al. 2021). Further, once established within a post-fire stand, aspen colonization may trigger change in plant-soil feedbacks that create fuel conditions conduce to lower intensity fire (Johnstone et al. 2020, Nesbit et al. 2023, Harris et al. 2025). These changes to the fire regime combined with aspen's propensity for rapid post-fire vegetative

regeneration can limit regeneration opportunities for conifers and promote the persistence of an aspen-dominated community (Johnstone et al. 2020, Walker et al. 2023).

The potential for aspen to colonize new areas through aspen seedling recruitment is broadly understood to depend on several factors. First, seed must disperse from the unburned edge or fire refugia. While aspen seedling establishment has been observed several kilometers from a live population, most seedling establishment occurs relative close to a parent tree (Kreider and Yocom 2021b). Given seed arrives, successful germination occurs on moist substrates, which are often located within microdepressions where water collects or near coarse woody debris that provides shade (Kreider and Yocom 2021b, Carter et al. 2024). In addition to adequate soil moisture, germinants require partial or direct sunlight to survive because aspen seeds lack an endosperm (Landhäusser et al. 2019). Thus seedling establishment is far more likely to occur at sites that were recently severely burned, where competition for light is limited (McIlroy and Shinneman 2020). While the root systems of young seedlings are developing and capable of accessing water close to the soil surface they are highly vulnerable to drought (Landhäusser et al. 2019) and so survival of young seedlings is highly dependent on post-fire climate conditions (Kreider and Yocom 2021a). Notably many of these environmental filters are also limiting to successful post-fire establishment of conifers (Stevens-Rumann and Morgan 2019), although most conifer seeds disperse far shorter distances (Davis et al. 2023). Thus, understanding how seed availability and environmental factors intersect to influence patterns of both aspen and seedling establishment is essential to predicting where fires may catalyze shifts from conifer to aspen dominance.

In this study, we make use of a large wildfire that burned across multiple forest types and environmental conditions to better understand patterns and drivers of conifer and aspen seedling establishment in the West. Specifically, we asked we asked (1) how does postfire regeneration of conifers and aspen vary across sites? (2) how are aspen and conifer seedlings distributed within sites? and (3) how do site and microsite conditions influence aspen seedling establishment? For question 1, we hypothesized that tree regeneration patterns would be driven by regeneration traits. Specifically, we expected that regeneration of most conifers would be limited two years following fire, but lodgepole pine seedlings would be relatively abundant in stands where it was present pre-fire due to the species' capacity to produce serotinous cones. We also expected that aspen seedlings would be widespread, but at relatively low densities due to the species' capacity to produce abundant light-weight seeds. For question 2, we expected that both aspen and conifer seedlings would be spatially clustered within sites, due to local variation in microclimate, soils, and seed availability. For question 3, we expected that aspen seedlings would be more likely to occur at high elevations, cooler and wetter aspects, and within sites with conifer seedlings, which likely indicate conditions were moisture availability is conducive to successful germination and initial survival. At the local scale, we hypothesized that aspen seedlings would be associated with microsite features associated with increased moisture availability, including the presence of CWD, concave topography, and substrates with high proportions of bryophyte cover.

METHODS

Study area

We surveyed tree regeneration across upper montane and subalpine forests that burned in the Cameron Peak Fire located in northern central Colorado (Fig. **1**). Over the period from August to December 2020, the fire burned across 845 square kilometers (MTBS Project 2024a). Approximately 39% of the fire burned at high severity (MTBS Project 2024b), including a wide gradient of elevation ranging from

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119 about 1645 to 3544 meters above sea level. Generally, winters are cold (1991-2020 mean January daily
120 minimum temperature: -0.2°C) and summers are hot (1991-2020 mean July daily maximum
121 temperature: 23.4°C), but across this elevation gradient there is considerable variation in climate. Mean
122 annual daily temperatures range from -1.4 to 9.3°C and total annual precipitation ranges from 361 to
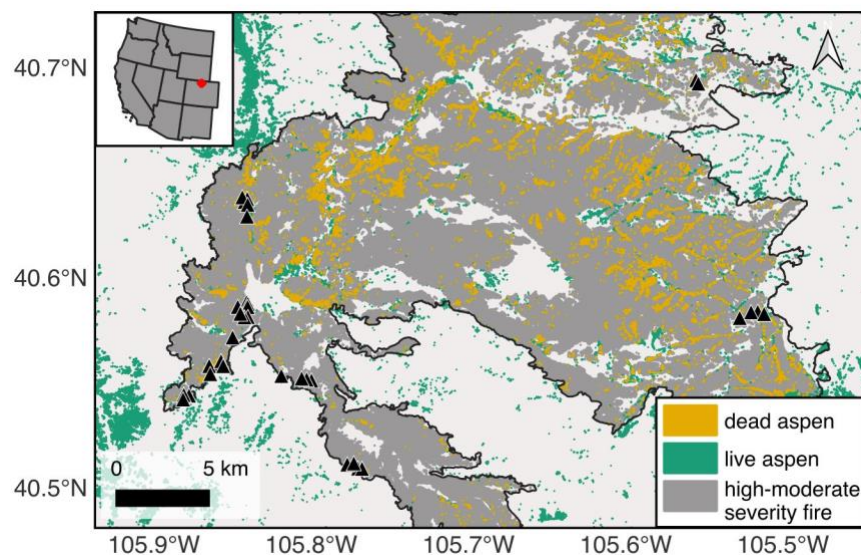123 1145 mm (1991-2020 means) (PRISM Climate Group 2021).

124

125 **Figure 1:** The study area, study sites (triangles), and the distribution of live and burned aspen. The inset
126 map displays the study area relative to western United States.

127 Pre-fire forest composition and structure within the burn scar of the Cameron Peak Fire scar also varied
128 with elevation. Lower elevation zones below 2800 m were characterized by dry and mesic montane
129 forests, dominated by ponderosa pine (*Pinus ponderosa*), with lesser components of Douglas-fir
130 (*Pseudotsuga menziesii*). Moderate and higher elevation stands between approximately 2800 – 3300 m
131 were made up of subalpine forest, dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir
132 (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). In the two decades prior to the fire, outbreaks
133 of mountain pine beetles (*Dendroctonus ponderosae*), spruce beetles (*Dendroctonus rufipennis)*, and
134 western balsam bark beetles have caused mortality of pine, Engelmann spruce, and subalpine fir,
135 respectively, across about 40% of the burned area (Rodman et al. 2021). Only about 3% of the area
136 burned was dominated by aspen prior to fire, most (~80%) of which occurred between 2235 and 2874 m
137 in elevation. About 37% of the aspen forest burned at high severity.

138 **Study sites.C**

139 We surveyed 34 sites in the summer of 2022 (Fig. **1**). Sites were randomly located using geospatial data
140 describing the extent and severity of the Cameron Peak Fire from the Monitoring Trends in Burn
141 Severity (MTBS) Project (2024b, 2024a) and the extent of pre-fire aspen cover from Cook et al. (2024).
142 We combined these data sources to identify areas that: (a) burned at high or moderate severity and (b)
143 were located >50 m and <1000 m away from a pre-fire patch of aspen. Sites were further limited to
144 accessible areas, defined as public land within 1000 m of a road or 500 m away from a trail and no more
145 than 1 km up the trail. To reduce the potential effects of psuedoreplication, all sites were located >400

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146   meters apart, or about twice as far as the minimum sampling distance used by Kreider et al. 2021
147   (2021a). Despite the extensive area burned, the accessible area was notably restricted by a limited road
148   network and postfire treatments (e.g., aerial mulching) and damage to infrastructure. Nonthelesss our
149   sample sites span broad gradients in elevation (2462 - 3255 m), mean annual daily temperature (-0.2 -
150   5.6°C), and annual total precipitation (431 - 1069 mm) (1991-2020 means) (Table S**1**).

151   **Field data collection**

152   At each site, we recorded the coordinates, elevation, slope, aspect, and pre-fire tree-species composition.
153   We then established two perpendicular 2 x 50 m transects that intersected at the midpoint (Andrus et al.
154   2021). We tallied the presence of all conifer seedlings, aspen seedlings, and aspen root suckers within
155   each transect and recorded their location along the transect within 2 x 2m subplots. Aspen seedlings
156   were differentiated from root suckers using methods outlined by Kreider et al. (2020), which have been
157   demonstrated to be more than 95% accurate (Kreider and Yocom 2021a) and were shown to be effective
158   in our study area (Carter et al. 2024). Along each transect, we also collected information on percent
159   herbaceous cover in three 1 x 1 m quadrats located every 20 m along each transect.

160   As a proxy for aspen seed availability, we also recorded the distance from plot center to live aspen trees.
161   Where live aspen were not visible in the field, we estimated the distance to live aspen using a GIS.
162   Specifically, we overlaid the MTBS map of fire severity (MTBS Project 2024b) on Cook et al.'s (Cook
163   et al. 2024) map of pre-fire aspen occurrence and assumed that any aspen stem that burned at moderate
164   or high severity was likely killed in the fire. We then calculated the distance from plot center to the
165   nearest live aspen pixel in R (R Core Team 2024) using the *terra* package (Hijmans 2022).

166   To test the hypothesis that microsite conditions influence aspen seedling establishment, we additionally
167   recorded information on proximity to coarse woody debris, substrate conditions, and microtopographic
168   condition for each aspen seedling. We characterized the microtopography as flat, concave, or convex
169   within 2.5 cm of seedling (hereafter 'small microtopography') and within 50 cm of seedling (hereafter
170   'large microtopography'). We also recorded the presence or absence of small (diameter = 2.5-10 cm)
171   and large (diameter >10 cm) coarse woody debris (CWD) within 10 cm of seedling. We also collected
172   microsite conditions at 5 meter intervals along each transect to serve as a baseline of the relative
173   abundance each condition across the site.

174   **Data analysis**

175   *Patterns of postfire regeneration*

176   We characterized patterns of post-fire conifer and aspen seedling regeneration using basic summary
177   statistics, including the proportion of plots with seedlings and the mean, median, minimum, and
178   maximum seedling densities in plots with seedlings. Summary statistics were calculated for each
179   individual species and pooled for all conifer seedlings. To understand how pre-fire forest composition
180   affects initial species composition, we also quantified the number of plots where each species was
181   present pre- and postfire.

182   *Clustering of seedlings*

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183   We tested if seedlings were clustered using a Chi-squared goodness-of-fit-test where the null hypothesis
184   was complete spatial randomness (i.e., that seedlings were equally distributed across the subplots).
185   Because clustering is difficult to detect at low densities, we only tested for clustering of seedlings in
186   plots with at least 1000 seedlings per ha (i.e., or on average 2 seedlings per subplot). To quantify
187   statistical significance, we used a bootstrapping approach with 1000 replications. We performed this
188   analysis separately for each site and tested for spatial randomness among aspen seedlings and then
189   among all conifer seedlings combined. We also tested if conifer and aspen seedlings were more likely to
190   co-occur using a Chi-squared goodness-of-fit-test where the null hypothesis was that conifer seedlings
191   were equally likely to occur in subplots with and without aspen seedlings. As above, we performed this
192   analysis separately for each site and used a bootstrapping approach with 1000 replication to determine
193   the statistical significance. All tests were performed in R (R Core Team 2024).

Site-level drivers of postfire aspen seedling regeneration

195   To understand the site factors that affect postfire aspen seedling establishment, we used a zero-inflated
196   generalized linear modeling approach with a negative binomial distribution to model the total number of
197   seedlings observed at a site. Zero-inflated models are useful for modeling an abundance of zeros (Zuur
198   et al. 2009), such as the high number of sites without postfire aspen seedlings that we observed here. As
199   predictor variables we tested elevation and heat load, which we calculated using site-level information
200   on slope, aspect, and latitude (McCune and Keon 2002). As an indicator of seed availability, we
201   included distance to live aspen. Finally, as indicators of site quality and competition, we tested for
202   effects of herbaceous cover and conifer seeding density, which was log transformed to the align with the
203   log transformation applied to the aspen seedling densities. Prior to building the model, all variables were
204   standardized to allow for easier comparison of coefficients. We trimmed the full model by dropping
205   each predictor variable individually and using likelihood ratio tests to compare the full model with the
206   reduced model (Zuur et al. 2009). Variables were trimmed first from the zero part of the model and then
207   the count component. As a measure of model performance, we calculated a pseudo R^2, defined as the
208   squared correlation between the model's actual and predicted response. To visualize the effects of each
209   significant predictor variables, we calculated the conditional predicted aspen seedling density as a
210   function of the predictor, holding all other predictor variables to their mean value. Analyses were
211   performed in R (R Core Team 2024) using the *glmmTMB* package (Brooks et al. 2017) to fit models, the
212   *lmtest* package (Zeileis and Hothorn 2002) to perform likelihood ratio tests, the *performance* package
213   (Lüdecke et al. 2021) to calculate pseudo R^2 and *marginaleffects* (Arel-Bundock et al. 2024) and *ggplot2*
214   packages (Wickham 2016) to construct and plot conditional predictions.

Microsite drivers of aspen seedling establishment

216   To understand if aspen seedlings preferentially established in different microsite conditions, we
217   followed the approach outlined by Kreider and Yocom (2021b). Briefly, we first modeled the probability
218   that aspen seedlings occur in each category of the predictor variable using a mixed effect multinomial
219   logistic regression that included a random intercept term of site identity. We then modeled the
220   probability that systematically surveyed points occurred in each category of the variable, also using a
221   using a mixed effect multinomial logistic regression that included a random intercept term of site
222   identity. We used these two models to quantify microsite preference following methods outlined by
223   Krieder and Yocom (2021b), where:

$$preference = \frac{P(occurence) - P(availabilty)}{P(availability)}$$

225 and *P(occurrence)* is the probability of seedling occurring in a given microsite condition and
226 *P(availability)* is the probability of a given microsite condition is available. Here, preference values
227 greater than zero indicate seedlings established in that microsite condition more often than expected
228 based on the systematic sample. Multinomial regression was performed in R (R Core Team 2024) using
229 the *mclogit* package (Elff 2023).

230 **RESULTS**

231 **Postfire seedling establishment within the Cameron Peak Fire**

232 Across sites that were dominated by conifers prior to fire and then severely burned, we found limited
233 seedling regeneration two years following fire (Table **1**). Aspen seedlings were present at 62% of sites,
234 with a mean density of 1155 seedlings per hectare. Conifer seedlings were present at a similar
235 proportion of sites (59% of plots), but at a lower density on average when present (Table **1**).

236 **Table 1:** The number of sites with postfire seedlings and measures of density trees per ha) for sites with
237 seedlings present.

species	n	mean	median	min	max
subalpine fir	1	150	150	150	150
lodgepole pine	16	384	250	50	1,350
Engelmann spruce	3	200	150	50	400
ponderosa pine	3	133	100	50	250
quaking aspen	21	1,155	300	50	7,850

238 Generally, the conifer species present in the postfire community reflected the pre-fire community.
239 Lodgepole pine seedlings were present at 55.6% of sites were lodgepole was present prior to fire (Fig.
240 **2**). In contrast, Engelmann spruce and subalpine fir seedlings were only present at 9.5% and 4.8% of
241 sites where they occurred prior to fire. Ponderosa pine occurred at 42.9% of sites and Douglas fir
242 seedlings were entirely absent postfire; however, the sample size for both species was small
243 ($n_{ponderosa\ pine}$=7 sites; $n_{Douglas\ fir}$=2 sites). postfire seedlings of lodgepole pine and Engelmann spruce were
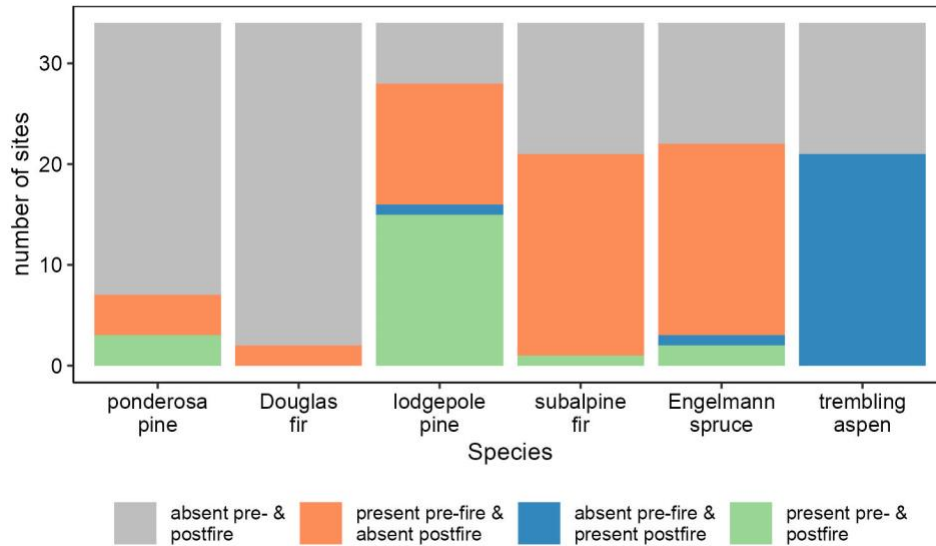244 both observed at one site where they were absent in the pre-fire community (Fig. **2**).

Figure 2: Patterns of postfire species presence by pre-fire species presence.

Clustering

Within sites with aspen seedlings, on average 12.1% of the fifty 2 x 2 m subplots contained aspen seedlings (mean=6 subplots; range=1 - 30 subplots). About 56% of aspen seedlings occurred in subplots with another aspen seedling, with densities ranging from 0.25 to 6.5 seedlings per square meter (mean=0.95 seedlings per square meter). Across the 6 sites with at least 1,000 aspen seedlings per hectare, aspen seedlings were significantly ($p<0.05$) clustered at all sites (Table S**2**).

Within sites with conifer seedlings, on average only 9.2% of the fifty 2 x 2 m subplots contained seedlings (mean=4.6 subplots; range=1 - 21 subplots). About 33% of conifer seedlings occurred in subplots with another conifer seedling and densities for subplots with conifer seedlings varied between 0.25 to 2 seedlings per square meter (mean=0.4 seedlings per square meter). We found multiple ponderosa pine seedlings in 17% of subplots with ponderosa pine seedlings, multiple lodgepole pine in 32% of subplots with lodgepole pine seedlings, multiple Engelmann spruce in 20% of subplots with Engelmann spruce, and multiple subalpine fir in 50% of subplots with subalpine fir. Across the 2 sites with at least 1,000 conifer seedlings per hectare, conifer seedlings were significantly ($p<0.05$) clustered at all sites (Table S**3**). Sites with at least 1,000 conifer seedlings per hectare were dominated by lodgepole pine, however at one of these sites we observed lodgepole and Engelmann spruce co-occurring in three of the seven subplots where spruce was present.

We also found that conifer seedlings were significantly ($p<0.05$) more likely to occur in subplots with aspen than expected by complete spatial randomness (Table S**3**). However, only two sites had sufficient densities of both aspen and conifer seedlings to test this hypothesis. At these sites we found most (67 - 89%) of the subplots with conifer seedlings also had aspen seedlings. Most of this co-occurrence included lodgepole pine; 21 out of 26 subplots had both lodgepole pine and aspen seedlings. However, Engelmann spruce co-occurred with aspen seedlings in three of the seven subplots where spruce seedlings were present.

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Site-level drivers of postfire aspen seedling density

Site-level variability in bioclimatic conditions influenced the density of aspen seedlings observed two-years following the Cameron Peak Fire. Our model of aspen seedling density explained a moderate amount of the variation (pseudo R^2= 0.42) and correctly predicted 95% of the sites where aspen seedlings were observed (20 of the 21 sites with aspen seedlings), but only 31 % of the absences (4 of the 13sites without aspen seedlings). In the zero component of the model, elevation was the only significant predictor (Table **2**). Sites without aspen seedlings occurred at lower elevations (standardized β = -0.79; standard error = 0.4; Fig. **3**A). In the count component of the model, elevation and the density of conifer seedlings were significantly related to aspen seedling density ($p<0.05$; Table **2**). Fig. **3**B-C). Density increased with elevation (standardized β = 0.73; standard error = 0.25; Fig. **3**B). Aspen seedling density also increased with the natural log of conifer seedling density (standardized β = 1.16; standard error = 0.23; Fig. **3**C).

Table 2: Summary of zero-inflated negative binomial model selection results for absence (zero model) and abundance (count model) of post fire aspen stems. χ2 test statistics and p-values are from likelihood ratio tests comparison the full model to a reduced model where the focal predictor is dropped. AIC values are for the reduced model (i.e., higher AIC indicates removing this variable reduces model fit).

| Component	Predictor	AIC	χ2	p
Zero	Elevation	379.6	4.96	0.026
Zero	Heat load	375.3	0.69	0.405
Zero	Herbaceous cover	375.5	0.94	0.332
Zero	Conifer seedling density	374.6	0.01	0.913
Zero	Seed-source distance	374.7	0.07	0.784
Count	Elevation	374.7	6.62	0.010
Count	Heat load	368.5	0.46	0.500
Count	Herbaceous cover	369.4	1.35	0.246
Count	Conifer seedling density	375.8	7.79	0.005
Count	Seed-source distance	368.2	0.19	0.663

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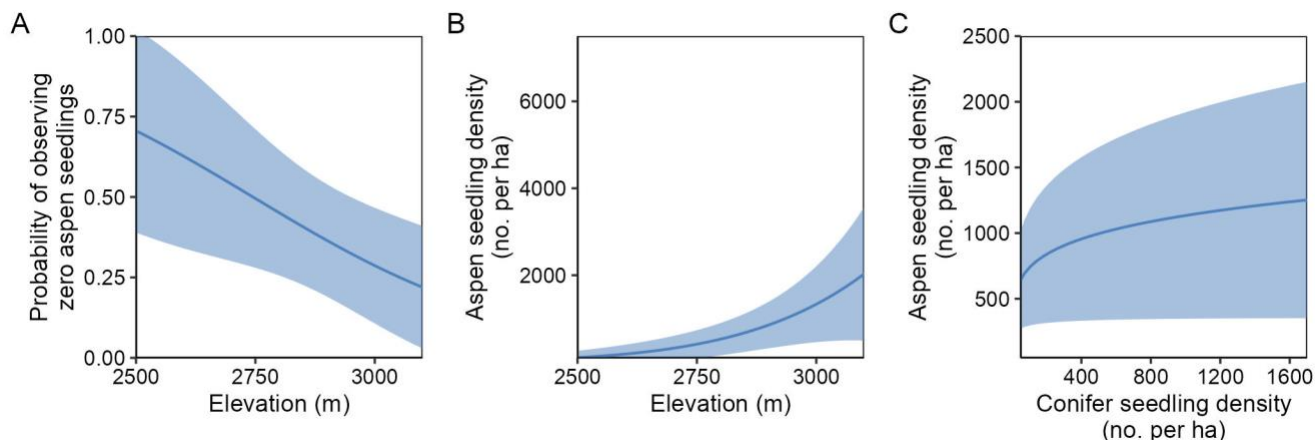
Figure 3: The predicted effects of elevation (A-B) and conifer seedling density (C) on patterns of aspen seedling density across the Cameron Peak Fire. In all panels, the shading illustrates the 95% confidence interval.

Microsite drivers of postfire aspen seedling establishment

Within sites with aspen seedlings, we found microsite conditions were important predictors of aspen seedling establishment (Fig. **4**). Notably, aspen seedlings were about 21.5 times more likely to occur on bryophytes than any other substrate type. Seedlings also preferentially established in large and small concavities, with preferences of 13.9 and 6.5, respectively. Finally, aspen seedlings were more likely to establish in microsites near large CWD than microsites with small CWD, small and large CWD, or no CWD (preference for large CWD = 4.1)
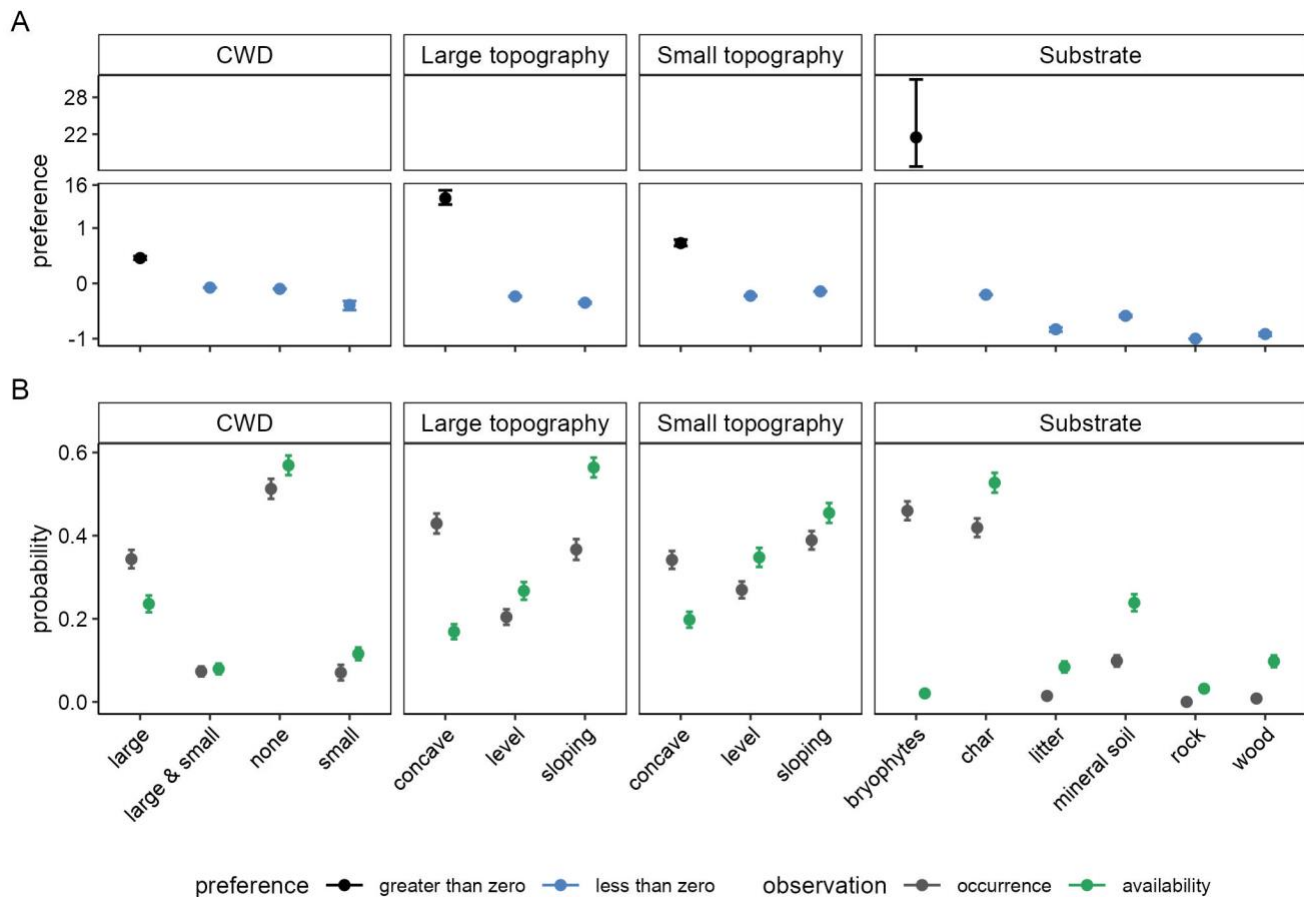
Figure 4: Aspen seedlings preferentially establish within certain microsite conditions. (A) Positive (black) and negative (blue) modeled aspen seedling microsite preferences. (B) Modeled probabilities of seedling occurrence in a given microsite condition (green) and the probability a given microsite condition is available (dark gray). In both A and B, error bars illustrate one standard error. Note that the y-axis in the substrate panel in part A is broken to better show the data.

DISCUSSION

Here we found widespread, but highly variable establishment of aspen seedlings across conifer forests that burned at high severity during the Cameron Peak Fire, despite the absence of aspen in the pre-fire stand. Aspen seedlings were more likely to occur at higher elevations, where they were often clustered within concave microsites, on bryophyte substrates, and near large coarse woody debris. Collectively, this adds to the support for the idea that cooler and wetter climate conditions promote aspen seedling establishment in recently burned ecosystems (Quinn and Wu 2001, Buma and Wessman 2012, Kreider and Yocom 2021a, 2021b). We also found aspen seedlings were more likely to occur at sites with greater postfire conifer seedling densities, consistent with previous research which has highlighted the potential for aspen to expand into recently burned conifer forests and shape the dynamics of burned ecosystems (Gill et al. 2017b, Nigro et al. 2022).

Distribution and abundance of aspen and conifer seedlings

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Across the Cameron Peak Fire, we found aspen seedlings at 62% of sites surveyed. This occupancy rate is similar to the highest fire-level occupancy rates reported by Kreider and Yocom (2021a), who sampled 15 fires spanning a latitudinal gradient from northern Arizona to northern Wyoming. Across this sample, they reported aspen seedlings in only 13% of sites, with occupancy rate for individual fires events varying from 0 to 61% (Kreider and Yocom 2021a). In the case of the Cameron Peak Fire, the high occupancy rates may be attributed to our sampling design, which included larger sampling area than Kreider and Yocom (2021a) and excluded areas that burned at low or moderate severity, where seedling establishment may be less likely (Turner et al. 2003, Gill et al. 2017b). The high occupancy rates may also reflect characteristics of the burned landscape (e.g., elevation).

At sites with aspen seedlings, our median density of 300 seedlings ha^{-1} and maximum density of 7850 seedlings ha^{-1} is comparable to median (range: 100-900; median across fires: 100 seedlings per ha^{-1}) and maximum (range: 100-9700; median across fires: 150 seedlings ha^{-1}) densities for the 15 fires surveyed by Kreider and Yocom (2021a). However, postfire establishment of aspen from seed can be extremely abundant. For example, following both the 2017 Brian Head and the 1998 Yellowstone fires aspen seedling densities exceeded 150,000 seedlings ha^{-1} (Kaye et al. 2003, Kreider and Yocom 2021b). Such dense postfire establishment of aspen can have important implications for postfire vegetation trajectories and rates. Yet, within the Cameron Peak fire only 38% (n= 8) of the sites with aspen seedlings surveyed here would meet local USFS requirements for restocking (741 seedlings per ha^{-1}) (USFS 1997), and thus may have more limited effects on the postfire ecology of this system.

Two years following fire, we found relatively low regeneration of subalpine fir, Engelmann spruce and ponderosa pine, and to a lesser extent lodgepole pine despite their presence in the pre-fire community. Compared to local USFS requirements for conifer restocking (370 seedlings per ha^{-1}) (USFS 1997), only six of our sites were stocked - five sites with lodgepole pine and one site where densities of both lodgepole pine and Engelmann spruce exceeded the stocking threshold. These low densities may have been due to the relatively the warm and dry weather in the two years post-fire. Such conditions have emerged as important constraints on postfire germination and initial survival of conifer seedlings in recent decades (Stevens-Rumann and Morgan 2019). Additionally, viable seed may have been limited by pre-fire outbreaks of bark beetles (Andrus et al. 2021, Rhoades et al. 2022, 2025), which caused widespread and severe mortality across the study area in the beginning of the 21st century (Rodman et al. 2021). While infilling of burned areas with conifers seedlings can continue for decades following the fire, seedling densities two-years following fire are often good predictors of recruitment failure in conifer forests across the West (Stevens-Rumann et al. 2018). Thus in the absence of human intervention, conifers may remain limited across the system. Nonetheless, further research is needed to understand how the forests may develop (Gill et al. 2017a).

While aspen seedling regeneration was not incredibly abundant across the Cameron Peak burn scar, densities of aspen seedlings often exceeded densities of conifer seedlings. Here we found aspen seedlings were present at 60% of the sites with conifer seedlings and outnumbered conifer seedlings at 83% of these sites. Further aspen seedlings and conifer seedlings were more commonly found clustered together within a site than expected by complete spatial randomness, highlighting shared environmental conditions suitable for regeneration. The co-occurrence of aspen and conifer seedlings both across and within sites suggests that rates and trajectories of postfire recovery may be shaped by competition between aspen and conifers.

Drivers of aspen seedling establishment

12

360 Across our study sites, aspen seedling occurrence and density increased with elevation. Higher
361 elevations are characterized by cooler summers and greater winter snowpack accumulation and
362 retention, which lower moisture stress. Low elevation sites, in addition to already being at the lower
363 bounds of aspen habitat suitability (Rehfeldt et al. 2009), were also characterized by greater herbaceous
364 cover, which may both out compete aspen seedlings and occupy the substrate preferred by seedlings
365 (Kreider and Yocom 2021a). Nonetheless, we observed aspen seedlings as low as 2462 m, where annual
366 precipitation averages 463 mm and mean daily temperature averages 5.6°C. In comparison, Kreider and
367 Yocom (2021a) reported postfire aspen seedling establishment was unlikely where average annual
368 precipitation values were less than 750 mm on average. Yet here we found 62 % of sites with aspen
369 seedlings normally received less than 750 mm precipitation annually. At these sites, microsite conditions
370 controlling soil moisture may be particularly important in controlling aspen regeneration.

371 Contrary to previous research which clearly shows that aspen seedling density is greater when live aspen
372 trees are nearby (Kreider and Yocom 2021a, 2021b), our modeling did not support this expectation. This
373 may because across the Cameron Peak fire, the distance from live aspen generally increased with
374 elevation, largely because aspen were more common at lower elevations prior to the fire and fire
375 severity increased with elevation (Fig. **S3**). As result, sites with higher climatic suitability were typically
376 at a greater distance from live seed sources. Such mismatches between landscape-patterns of climatic
377 suitability and seed availability may limit the potential for aspen to expand into new habitats.

378 At the microsite scale, seedling occurrence was related to the bryophyte cover, the presence of coarse
379 woody debris, and concave microtopography, which may have connections to the accumulation and
380 retention of seeds, moisture, and nutrients (Fairweather et al. 2014, Kreider and Yocom 2021b). Fallen
381 logs or other large debris and local concavities may serve to collect both seeds and moisture necessary
382 for successful establishment and survival in the first 1-3 growing seasons (Fairweather et al. 2014).
383 Importantly, microsite conditions favorable to aspen establishment were not evenly distributed across
384 the fire. For example, we identified bryophytes as the dominant substrate at 1% of random samples,
385 while we found 46% of aspen seedlings had established on bryophytes. Understanding how suitable
386 microsites are distributed across landscapes will be central to predicting postfire regeneration of aspen
387 and understanding how forest change following wildfire.

388 **CONCLUSIONS**

389 Increased fire frequency, severity, and extent in western North America may exceed the capacity of
390 some formerly conifer-dominant forests to maintain historical distributions (Coop et al. 2020), while
391 conditions following high severity burns may allow establishment of aspen seedlings both within and
392 outside of pre-fire aspen populations (Kreider and Yocom 2021a, Nigro et al. 2022). We observed this
393 phenomenon in high severity zones of the Cameron Peak Fire, particularly in areas where topographic
394 heterogenity and post-fire legacies resulted in increased moisture availability. Concurrent with aspen
395 seedling regeneration, we found low overall regeneration of conifer species relative to aspen. Across our
396 system, limited conifer regeneration likely results from warm and dry weather and pre-fire outbreaks of
397 bark beetles that caused extensive tree mortality - conditions that are expected to become more common
398 with climate change (Bentz et al. 2010, IPCC 2021). These trends coupled with changing fire regimes
399 and our observations, along with a growing body of research on aspen seedling regeneration in the West
400 (e.g., Gill et al. 2017b, Andrus et al. 2021, Kreider and Yocom 2021a, Nigro et al. 2022), suggest that
401 aspen may increasing shape post-fire ecology across the West.

13

402 LIST OF ABBREVIATIONS

403 CWD: coarse woody debris

404 DECLARATIONS

405 **Ethics approval and consent to participate**

406 Not applicable

407 **Consent for publication**

408 Not applicable

409 **Availability of data and material**

410 The datasets generated and/or analyzed during the current study are available in Dryad Research Data
411 Repository, link (REF)

412 **Competing interests**

413 The authors declare that they have no competing interests.

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416 **Authors' contributions**

417 **SVC**: conceptualization (equal); methodology (equal); data collection (lead); methods (supporting);
418 writing - original draft (equal), writing - review and editing (equal); **SJH**: conceptualization (equal);
419 methodology (equal); data collection (supporting); methods (lead); writing - original draft (equal),
420 writing - review and editing (equal). All authors read and approved the final manuscript.

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19

SUPPLEMENTARY MATERIAL

585 **Table S 1:** Characteristics of study sites sampled within the Cameron Peak Fire. Annual precipitation
586 and temperature values are 1991-2010 normals from PRISM (2021).

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Distance to live aspen (m)	Aspen seedling density (no. per ha)	Conifer seedling density (no. per ha)
10	40.588	-105.856	2,898	1.8	584	210	0	250
11	40.593	-105.861	2,901	1.8	584	783	100	0
12	40.590	-105.859	2,926	1.8	584	390	150	0
13	40.564	-105.876	3,051	1.3	820	114	0	50
14	40.560	-105.874	3,040	1.2	867	141	50	0
15	40.566	-105.868	3,025	1.3	761	331	0	0
16	40.564	-105.867	3,012	1.3	761	228	0	0
17	40.646	-105.866	2,715	2.8	546	104	50	0
18	40.642	-105.862	2,739	2.6	488	260	0	50
19	40.637	-105.861	2,751	2.4	502	158	100	0
2	40.616	-105.530	2,519	5.1	459	349	0	250
20	40.578	-105.863	2,959	1.4	723	461	3,000	50
21	40.562	-105.829	3,029	1.3	804	361	400	300
22	40.548	-105.886	3,206	0.6	1,000	192	50	0
23	40.549	-105.890	3,259	-0.2	1,069	156	1,450	0
24	40.546	-105.890	3,199	-0.2	1,069	156	100	0
25	40.562	-105.810	3,068	1.3	712	808	3,050	1,300
26	40.562	-105.813	3,099	1.3	762	660	800	500
27	40.562	-105.816	3,090	1.3	762	594	800	250
29	40.612	-105.541	2,599	5.1	458	436	0	100
3	40.616	-105.534	2,546	5.1	459	358	0	0
30	40.615	-105.526	2,462	5.6	463	132	100	50
31	40.724	-105.584	2,574	4.9	431	190	0	0

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Distance to live aspen (m)	Aspen seedling density (no. per ha)	Conifer seedling density (no. per ha)
32	40.722	-105.582	2,611	4.9	431	379	0	0
34	40.522	-105.774	3,106	0.6	786	851	1,500	150
35	40.522	-105.772	3,093	0.6	786	869	400	0
37	40.523	-105.781	3,119	0.6	804	1,097	0	150
38	40.524	-105.777	3,154	0.6	786	1,107	7,850	1,750
4	40.596	-105.856	2,850	1.8	584	721	0	650
5	40.595	-105.855	2,825	1.8	584	605	50	450
6	40.594	-105.855	2,835	1.8	584	541	300	250
7	40.645	-105.862	2,710	2.6	488	201	3,800	450
8	40.643	-105.864	2,724	2.8	546	63	150	250
9	40.589	-105.854	2,865	1.8	584	348	0	50

587

Table S 2: Summary of tests of complete spatial randomness for aspen seedlings.

Site	density (no. per ha)	χ2	p
7	3,800	601.6	0.001
20	3,000	586.7	0.001
23	1,450	441.7	0.001
25	3,050	502.1	0.001
34	1,500	86.7	0.003
38	7,850	237.6	0.001

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590

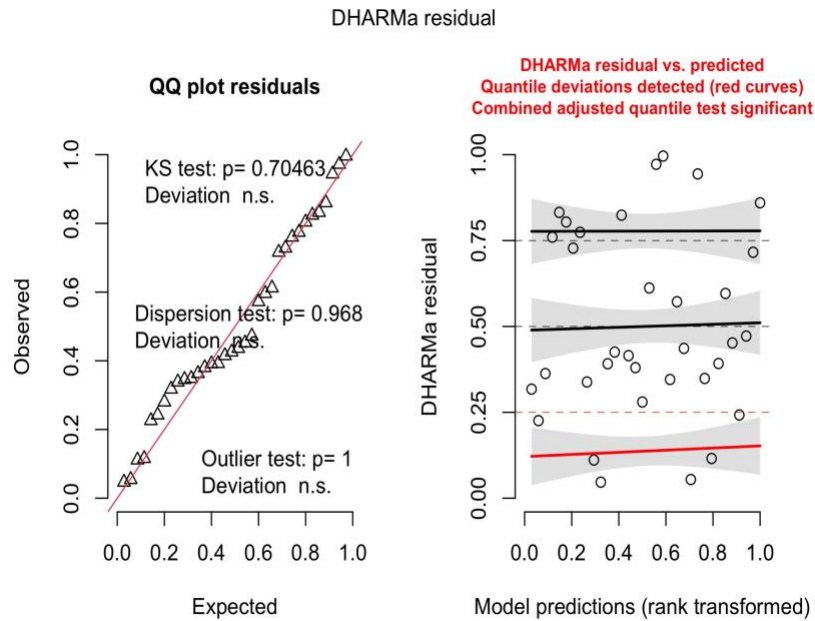**Table S 3:** Summary of tests of complete spatial randomness for conifer seedlings.

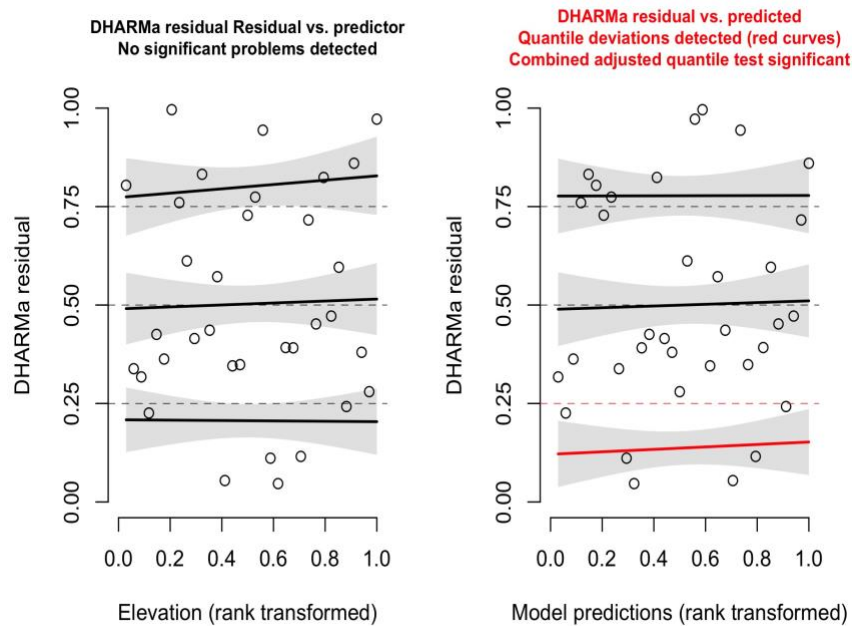| Site	density (no. per ha)	χ2	p
25	1,300	231.7	0.001
38	1,750	83.6	0.002

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592

Table S 3: Summary of tests of independence of aspen and conifer seedlings.

Site	conifer density (no. per ha)	aspen density (no. per ha)	χ2	p
25	1,300	3,050	22.15	0.001
38	1,750	7,850	4.83	0.039

22

DHARMa residual

QQ plot residuals

KS test: p= 0.70463
Deviation n.s.

Dispersion test: p= 0.968
Deviation n.s.

Outlier test: p= 1
Deviation n.s.

Observed

Expected

**DHARMa residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant**

DHARMa residual

Model predictions (rank transformed)

593

Figure S1: Residual diagnostic plots from the zero-inflated negative binomial model of aspen seedling density. Plots were generated using the DHARMa package (Hartig 2024).

**DHARMa residual Residual vs. predictor
No significant problems detected**

DHARMa residual

Elevation (rank transformed)

**DHARMa residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant**

DHARMa residual

Model predictions (rank transformed)

596

Figure S2: Plots of the simulated residuals from the zero-inflated negative binomial model of aspen seedling density as a function of elevation (left) and conifer seedling density (right). Plots were generated using the DHARMa package (Hartig 2024).

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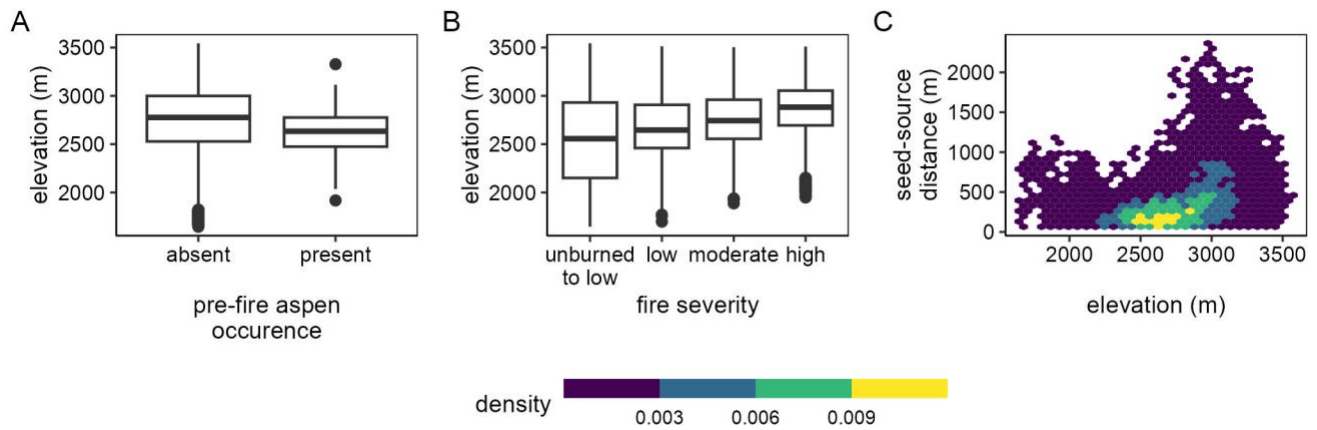
Figure S3: The relationship between elevation and aspen's distribution across the area burned in the Cameron Peak Fire. A) Boxplots comparing the elevation range of areas with and without aspen prior to the fire. B) Boxplots comparing the elevation by fire severity. C) The density of observations for areas that burned in the Cameron Peak fire that were greater than 50 m from live aspen and less than 1000 km from live aspen prior to the fire by elevation and distance to seed source.