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RESEARCH ARTICLE

Wildfire catalyzes upward range expansion of trembling aspen in southern Rocky Mountain beetle-killed forests

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Abstract

Aim: Climate warming is expected to drive upward and poleward shifts at the leading edge of tree species ranges. Disturbance has the potential to accelerate these shifts by altering biotic and abiotic conditions, though this potential is likely to vary by disturbance type. In this study, we assessed whether recent wildfires and spruce beetle outbreaks promoted upward range expansion of trembling aspen.

Location: The San Juan Mountains of southern Colorado, USA (37°34′–37°50′N, 106°49′–107°21′W).

Taxon: *Populus tremuloides*.

Methods: We used aerial imagery to determine the upper elevational limit of adult aspen and conducted seedling surveys at and above this upper limit in burned and unburned areas, which had already incurred high canopy mortality due to spruce bark beetle (*Dendroctonus rufipennis*) outbreaks. We compared characteristics of burned versus unburned bark beetle-killed sites and assessed microsite conditions related to aspen seedling establishment using generalized linear models and interaction indices.

Results: Aspen seedling establishment occurred upslope of its previous range within burns, but not in unburned areas, despite severe beetle-driven canopy mortality across all sites before the fire. Aspen seedling establishment was associated more with the light and mineral soil created by fire than the presence of nearby seed sources. Aspen seedlings were associated with nurse objects such as logs and rocks at the highest elevations, where these objects may ameliorate a range of stressors associated with the high elevation range boundary.

Main conclusions: Not all disturbance types are equal in promoting tree species migrations at the leading edge. Range shifts can be highly localized, and microsites are important for driving local range expansions in transitional environments. The mosaic of future disturbances across the landscape will drive forest compositional shifts, depending on the disturbance types and the species they promote.

KEYWORDS
compound disturbance, global change ecology, leading edge, microsite, nurse objects, post-fire regeneration, range expansion, tree migration

1 | INTRODUCTION

Climate warming and associated increases in extent and frequency of high severity disturbance events will reshape the vegetation patterns seen on the landscape today (Millar & Stephenson, 2015). There is considerable evidence that changes in past climate prompted range shifts and genetic adaptation in plant species (Carter et al., 2017; Davis & Shaw, 2001); therefore, current and future increases in temperatures are expected to result in poleward migrations and upward shifts in elevation of species ranges as they track changes in climate (Chen et al., 2011; Harsch et al., 2009; Mamet et al., 2019). Evidence for recent upward migration of plants in North America and Europe in response to climate warming is extensive (Brusca et al., 2013; Chen et al., 2011; Gottfried et al., 2012; Parolo & Rossi, 2008), though significant lags have been reported for long-lived woody species (Gray & Hamann, 2013; Lenoir et al., 2008; Rees et al., 2020; Renwick & Rocca, 2015).

Lags in elevational shifts of plants may occur because of geographic barriers (Davis & Shaw, 2001), biotic competition with resident plant communities (Brooker, 2006), lack of appropriate environmental conditions for seed production and/or germination (Brown et al., 2019), and microrefugia or evolutionary adaptation allowing population persistence under seemingly unfavourable climate conditions (Alexander et al., 2018; Renwick & Rocca, 2015). Remnant populations that continue to persist as the climate becomes unfavourable can contribute to migration lags by maintaining environmental conditions that favour continued establishment of the remnant species, through competitive interactions and by reducing the availability of establishment microsites for newly colonizing species, especially those that are shade-intolerant (Eriksson, 2000; Svenning & Sandel, 2013). Long-lived tree species are especially likely to retain remnant populations as not only do they have long lifecycles, but adults are typically able to persist in a wider range of environmental conditions relative to seedlings, due to extensive carbon reserves and large root systems (Jackson et al., 2009; Svenning & Sandel, 2013).

High-severity disturbances can remove some of these barriers to range shifts by reducing biotic competition, removing remnant populations, and altering abiotic conditions. Most forest disturbances cause adult tree mortality, which, when extensive, can eliminate the ability of the forest canopy to buffer the understory from temperature extremes (Arx et al., 2013; Carlson et al., 2021; Davis et al., 2019). This is likely to result in the development of a plant community that is more warm-adapted, as all regenerating species will be exposed to increasingly warmer temperatures under continued climate warming. In this way, inertia in tree species range shifts may be overcome rapidly, as the sudden removal of remnant tree populations produces novel climate conditions for regeneration and survival (Allen & Breshears, 1998; Dullinger et al., 2012; Lenoir & Svenning, 2015). Shade-intolerant species may require high-severity disturbance events at the leading edges of their ranges (the range margins expected to expand with climate warming) in order to overcome 'establishment lags' and migrate with climate change (Alexander et al., 2018; Loehle, 2003). Observed and predicted increases in the extent and frequency of high-severity disturbance in the western US (Keyser & Westerling, 2019; Millar & Stephenson, 2015; Westerling, 2016) could, therefore, promote range expansion of shade-intolerant tree species that were previously unable to establish beneath closed forest canopies.

Variation in disturbance type, size and severity create unique environments that allow different types of colonizing species to establish (Buma & Wessman, 2012). For a disturbance to catalyse a range shift of a particular species, it must create microsite conditions that align with the regeneration requirements of the migrating species and that species must have adequate dispersal capacity for propagules to reach areas within the disturbance footprint (Alexander et al., 2018). Therefore, disturbances that are large and cause abundant tree mortality are most likely to catalyse range shifts in species with high light requirements and widely dispersed seeds. The establishment of species that require reduced litter and organic layers for regeneration may be best promoted by wildfire, which can generate large expanses of bare mineral soil (Johnstone & Chapin, 2006). In contrast, disturbances such as insect outbreaks, disease, and drought can increase light and moisture availability but maintain or even increase dense litter layers adverse to the establishment of many species (Astrup et al., 2008; Carlson et al., 2020; DeRose & Long, 2010). Insect outbreaks are also often species-specific such that only certain tree species are killed, whereas fires are more likely to cause mortality across species, resulting in different post-disturbance tree species composition. Accordingly, a mechanistic framework for severe wildfire to catalyse tree species range shifts is well developed; however, surprisingly few examples have been observed (Brice et al., 2020; Crausbay et al., 2017; Johnstone & Chapin, 2003; Wang et al., 2019), and we lack contrasts between the effects of fire and other disturbance types.

In this study, we assessed whether recent wildfires and bark beetle-caused tree mortality led to upward range expansion of trembling aspen (*Populus tremuloides* Michx., hereafter 'aspen'), a widely distributed and ecologically important shade-intolerant species in North America. Aspen's life history traits suggest that range expansion at its leading edge may require a catalyst such as wildfire (Brown et al., 2006; Kulakowski et al., 2004; Romme et al., 2001). Aspen's primary mode of reproduction is asexual, via resprouting from its roots in response to canopy mortality; however, it also has small, wind-dispersed seeds and studies have documented aspen regeneration from seed after disturbance events (Fairweather et al., 2014; Kreider & Yocom, 2021; Landhäusser et al., 2010; Quinn & Wu, 2001; Romme et al., 1997). Aspen seedling establishment is associated with moderate temperatures, high-light environments, thin soil organic matter layers and microsites that capture moisture (Lafleur et al., 2015; Landhäusser et al., 2019; McDonough, 1979; Schott et al., 2014). Thus, seedlings are most often found in severely burned areas, where these seedbed requirements and nurse objects (in the form of snags and down logs) are more prevalent (Coop & Schoettle, 2009; Johnstone & Chapin, 2006; Turner et al., 2003).

Bioclimatic modelling studies have projected an upward and northward shift in aspen's distribution (eg, Gray & Hamann, 2013; Rehfeldt et al., 2009; Worrall et al., 2013), yet few studies have documented upward range shifts (Landhäusser et al., 2010), especially in the context of multiple, high-severity disturbances. Through a field survey in burned and unburned beetle-killed forests in the southern Rocky Mountains, we sought to answer the following questions: (1) Is aspen's upper elevational limit expanding upslope, and does that vary as a function of disturbance type? and (2) What microsite conditions promote aspen upslope expansion within disturbances? We hypothesized that aspen has expanded upslope of its previous range limit via seed due to recent climate warming, that aspen seedling establishment at high elevations is greater in burned areas due to greater light levels and more bare mineral soil, and that aspen seedlings preferentially establish in microsites buffered by nurse objects, areas with less litter and less competing vegetation, and areas with higher light levels.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in the San Juan Mountains of southern Colorado, USA on the Divide Ranger District of the Rio Grande National Forest (Figure 1). The study area's mean annual temperature from 1981 to 2010 averaged 1.8°C and mean annual precipitation averaged 849 mm (PRISM Climate Group, 2012). Surveys were conducted between 3280 and 3770 m in elevation. High elevation areas receive precipitation in the form of monsoonal rains from July to September and snow from October to April, with a short dry period from May to June, but precipitation can be highly variable from year to year (Goble et al., 2016). The annual mean temperature in the study area has increased 0.8°C in the past 100 years, while the annual minimum temperature has increased 1.8°C, and the annual maximum temperature has experienced little change in the past century (National Climatic Data Center, 2020).

The study was focused within and around the Papoose and West Fork East fire scars which together burned approximately 32,954 hectares in 2013 as part of the lightning-ignited West Fork Fire Complex. The pre-fire forest composition was dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), with a substantial aspen component occurring both as large stands spanning thousands of hectares and as small patches intermixed within conifer forests. Areas above the treeline are dominated by shrubland, dry tundra and grassland (LANDFIRE, 2012). The study area experienced extensive mortality of Engelmann spruce due to a spruce beetle (*Dendroctonus rufipennis*) outbreak, first detected in the area in 2004 (Carlson et al., 2017). By the time of the fire, over 88% of the area that would burn contained large contiguous patches of beetle-killed trees and the adjacent unburned areas similarly had extensive spruce beetle-caused tree mortality (Savage et al., 2017; USDA Forest Service, 2013). The West Fork Fire Complex caused further tree mortality, resulting in many areas with no or very low overstory tree cover (Carlson et al., 2017; Savage et al., 2017).

Aspen stands near the species upper elevational limit that existed before the West Fork Fire Complex (referred to hereafter as pre-fire aspen) were selected for sampling. These aspen stands likely established anywhere from 140 to 300 years ago, as pre-EuroAmerican settlement fire rotations in high-elevation spruce-fir forest types

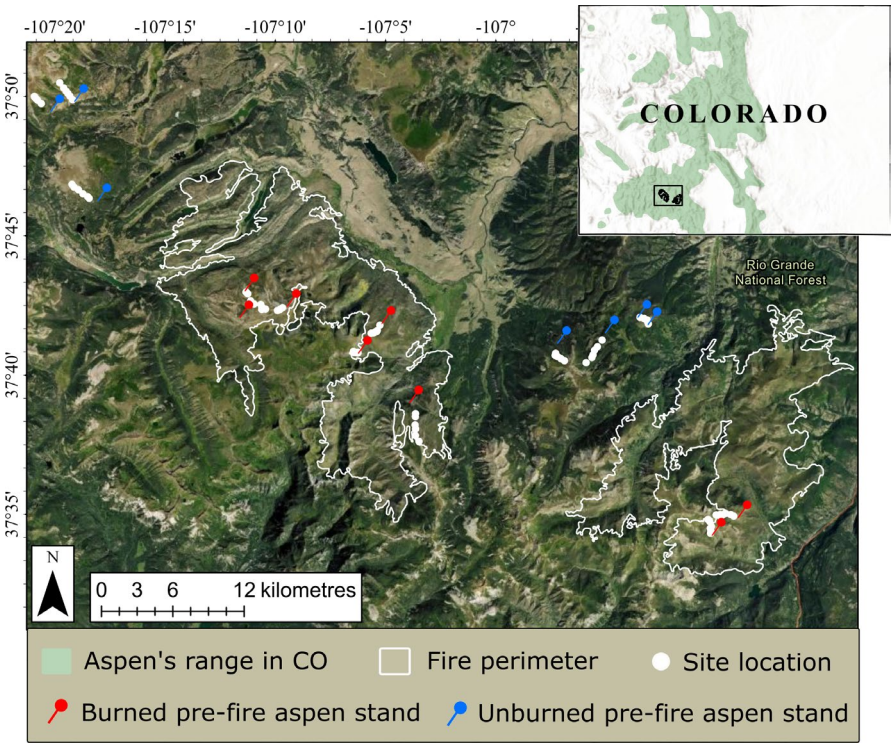

FIGURE 1 Map of the study area and aspen seedling survey locations in the Rio Grande National Forest, Colorado, USA. The rectangle on the locator map in the upper right corner encapsulates the West Fork East and Papoose fires (outlined in white), where the study was conducted. The main map displays the pre-fire aspen stands with a pushpin symbol, where colour denotes whether the stand was burned (red) or not (blue) in the 2013 West Fork Fire Complex. The satellite imagery displayed is the NAIP Imagery basemap from ArcGIS Pro and the projection is Mercator Auxillary Sphere

were centuries-long (300 years or more) and studies from the area have dated the most recent large-scale stand-replacing fire to have occurred in the 1870s (Margolis et al., 2007; Romme et al., 2001, 2009; Sibold et al., 2006). Therefore, the pre-fire aspen stands in this study likely established when the climate was more than 0.8°C cooler than the current average (National Climatic Data Center, 2020).

2.2 | Determination of pre-fire upper elevational limit

To determine the upper elevational limit of aspen in the study area prior to the 2013 wildfires, high-resolution aerial imagery (ArcGIS World Imagery Basemap January 2014 release; 0.3-m resolution) was assessed to identify aspen presence/absence from 7494 circular plots placed along 520 randomly generated upslope transects that spanned from 3200 m elevation to the highest mountaintops in the study region (see Appendix S1 in Supporting Information for details). We tested the accuracy of our ability to visually determine aspen presence by field sampling a subset of these plots ($n = 400$) for aspen presence (at least one aspen tree within the plot). We determined our overall classification accuracy (total number of correctly classified plots divided by all plots) was 94%, with most classification errors being those of omission (see Appendix S1), likely due to the challenges of detecting smaller, subdominant canopy aspen. Overall, the high classification accuracy indicates that our visual assessment of aerial imagery was effective at detecting aspen presence but was limited to canopy-dominant or co-dominant aspen stands.

The upper elevational limit of pre-fire adult aspen in the study area was calculated in two ways. First, using all sample plots containing aspen, the "upper inner fence" of the data were calculated as:

$$Q3\,(\text{third quartile elevation}) + 1.5 \times \text{IQR}\,(\text{interquartile range})$$

to capture the upper limit of the data without including mild outliers (Ott & Longnecker, 2015). Using this approach, we determined that prior to the 2013 wildfires, the elevational limit of aspen in our study area was 3506 m, and only 10 plots containing aspen occurred above this limit (99th quantile). Second, the maximum elevation where adult aspen was identified (3568 m) was used as a more liberal estimate of the pre-fire upper limit.

2.3 | Seedling surveys

To assess whether aspen upslope expansion has occurred following fire across our study area, we field-sampled a total of 47 burned and 41 unburned sites across eight burned and seven unburned elevational transects (Figure 1). Although the unburned sites did not experience mortality from the West Fork Fire Complex, all were impacted by the spruce beetle outbreak of the 2000s and therefore still experienced severe canopy mortality before our survey. From the aerial imagery analysis, we identified locations where aspen existed at or near its conservative upper limit (3506 m) prior to the fire. From the locations of each of these aspen stands, an elevational transect was established running upslope to the top of the mountain or a total increase of 240 m in elevation, whichever occurred first, maintaining the same aspect. The first site on each elevational transect was established immediately upslope and adjacent to the pre-fire aspen stand, though one of these first sites was determined to be hazardous and therefore excluded from the analysis. Subsequent sites were established every 40 m of elevation gain on the transects, which translated to 82–1226 m of horizontal distance on the ground. Minor adjustments to this protocol were necessary on a few sites to avoid hazardous conditions or to keep the elevational transect in its intended burn category. Slope, aspect, elevation, latitude, and longitude were recorded for each site in the field. Linear distance to the nearest live adult aspen stand was calculated in ArcMap using post-fire (2016 and 2018) aerial imagery to find the nearest stands.

At each site, belt transects measuring 50-m long by 8-m wide were established horizontally across the slope and searched for aspen juveniles (< 1.4-m tall). The exception to this was at the pre-fire aspen stand sites (the lowest site on each elevational transect), where variable-width belt transects measuring 50 m in length were established. These belt transects were a minimum of 0.5-m wide and were widened by 0.5 m until at least 14 aspen juveniles were found, or a maximum width of 8 m was surveyed. This was done to account for a large number of aspen suckers at these pre-fire aspen-dominated sites.

For each aspen juvenile found at a site, we recorded whether it was a seedling or sucker by gently excavating the roots. Aspen suckers sprout from lateral roots that can usually be found within 10 cm of the soil surface and can extend up to 30 m away from the parent stem (Day, 1944; USDA & NRCS, 2020). Therefore, the presence of a lateral root within 10 cm of the soil surface on a juvenile surrounded by other aspen juveniles indicated sucker status. Seedlings were characterized by multiple fine roots with no thick lateral root and generally occurred in isolation away from clumps of other aspen juveniles (as in Fairweather et al., 2014). In addition, we excavated one to five of the aspen seedlings found across each elevational transect and confirmed that they had branching, fine root systems characteristic of aspen established from seed (Day, 1944). The height and diameter at the soil surface were measured for each juvenile encountered, and any browse damage was noted. Microsite characteristics within 5 cm of the rooting location were recorded for each juvenile, including the presence or absence of a nurse object (defined here as rocks and logs > 5-cm diameter), the substrate type, the presence and depth of litter, and the presence or absence of vegetation. Canopy cover above the juvenile was measured with a spherical densiometer.

Across the 50-m length of the belt transect, the line point-intercept method was used to quantify the abundance of nurse objects, substrates, litter, understory vegetation, and canopy cover at the site. A pin flag was dropped every 0.5 m and all vegetation touching the pin flag (or touching the imaginary line

ascending from the pin flag) was recorded according to functional group (grass, forb, shrub, tree) and status (alive or dead). If multiple species of the same functional group touched the pin, the functional group was only recorded once for that point. Substrate type (soil, duff, boulder—rocks > 20-cm diameter and not easily lifted, or coarse woody debris [CWD]—wood > 20-cm diameter and not easily lifted), and presence of rocks (> 5-cm diameter and easily lifted), wood (> 5-mm diameter and easily lifted) and litter at each point was also recorded. The per cent cover of all vegetation, substrate types and nurse objects at each site was calculated by dividing the number of points where the vegetation/substrate was recorded by the total number of points sampled ($n = 100$) and multiplying this by 100. A point classified as "bare soil" in the analysis had to have a substrate of soil and no litter, duff, moss, rock or wood present at the point. Stand structure was additionally measured in three 100-m^2 circular plots (5.64-m radius) centred on the middle of the belt transect at 7, 25 and 43 m. The diameter at breast height, height, and status (alive or dead) were recorded for each tree within the circular plot.

2.4 | Statistical analyses—Upslope expansion and fire effects

Aspen upslope expansion was evaluated at local and regional levels. Local expansion was indicated by aspen seedlings growing above the pre-fire aspen stand identified on each elevational transect. The elevation of the pre-fire aspen stand on each elevational transect was subtracted from the maximum elevation where aspen seedlings were found on that elevational transect to calculate the local expansion. The difference between the pre-fire adult aspen upper elevational limit and post-fire seedling elevational limit across the study area was used to quantify regional upward expansion. The upper inner fence of the elevations where aspen seedlings were found in the field was 3740 m and exceeded the maximum recorded elevation of seedlings in the field due to the small number of observations ($n = 15$) and lack of outliers. More seedling observations would be needed to determine if this is an appropriate estimate of seedling upper elevational limit; therefore, we used a more realistic estimate of the seedling upper limit (the actual maximum recorded elevation) to quantify regional expansion. Due to the retrospective nature of this study and limited satellite imagery resolution, the upper limit of aspen juveniles prior to the fire in burned areas is unknown; however, if seedlings did exist above the pre-fire adult elevational limit before the fire, they would represent the same generation of aspen reproduction as the seedlings documented in this study (only 6 years post-fire) and would be picked up in our surveys of unburned areas.

Linear mixed-effects models were used to assess the effect of disturbance type (burned/beetle-impacted vs. unburned/beetle-impacted) on several site characteristics hypothesized to influence aspen seedling establishment. Only data from sites surveyed above the pre-fire aspen stands were used to characterize the upslope environment under burned and unburned beetle-impacted conditions. The predictor variable in all models was the burn category, represented as a fixed effect. The elevational transect was included as a random intercept to account for clustering among sites within each elevational transect and to account for differences due to the position within the burned landscape. The response variables tested were distance to nearest seed source, % canopy cover, % duff, % bare soil, % CWD, and % understory vegetation. Assumptions of linear regression were checked for all models before analysis. Per cent CWD, duff, and bare soil were log-transformed before analysis to meet assumptions of normality. Per cent dead trees from the stand structure plots and live Engelmann spruce canopy cover (from Savage et al. [2017] data) were calculated for unburned/beetle-impacted and burned sites with trees to compare canopy loss due to spruce beetle alone versus beetle-kill and wildfire. All models were performed in the 'lme4' package in R version 3.6.1 (Bates et al., 2014).

A generalized linear mixed-effects model (GLMM) was used to assess the influence of site characteristics on aspen seedling abundance. No seedlings were found in unburned/beetle-impacted sites; therefore, we analysed burned sites above the pre-fire aspen stands only. The number of aspen seedlings encountered in the 50 × 8-meter belt was used as the response variable and potential predictor variables included distance to nearest seed source, % bare soil, % CWD, % understory vegetation, heat load index, elevation and burn severity at the site. Per cent canopy cover and % duff were not considered for predictor variables in the GLMM because there was little variation between burned sites in these variables and the GLMM was aimed at teasing apart the factors driving variable aspen seedling abundance among burned sites. Heat load index was calculated following Lutz et al. (2010) (adapted from McCune & Keon, 2002) and integrates latitude, slope, and aspect into a unitless index of solar radiation at a site. Burn severity was represented by the relativized differenced Normalized Burn Ratio (RdNBR) (Miller & Thode, 2007) using data obtained from Monitoring Trends in Burn Severity (Eidenshink et al., 2007; MTBS Project, 2018). All predictor variables were centred (mean subtracted from value) and scaled (centred value divided by its standard deviation) to ease model convergence and comparison between variables. The elevational transect was included as a random intercept. The model was fit to the seedling count data with a Poisson error structure. We performed parametric bootstrapping to generate 1000 new datasets based on the model to assess model fit. The true number of zero responses in the data was captured by the simulated datasets, indicating no zero inflation. The sum of squared Pearson residuals from the bootstrap samples also captured the sum of squared residuals from the actual data, indicating that there was no overdispersion and the Poisson error structure was appropriate (Harrison et al., 2018). We, therefore, used a GLMM with Poisson error structure using the 'lme4' package in R (Bates et al., 2014). We performed variable selection for this model by comparing all subsets of models with the five potential predictor variables listed above that we hypothesized would be most important in driving aspen seedling abundance and selected the final model as the one with the lowest AICc.

2.5 | Statistical analyses—Microsite association of aspen seedlings

Interaction index (*I*), as described in Armas et al. (2004), was used to measure aspen seedling associations with bare soil, nearby vegetation, and nurse objects:

$$I = \frac{D_m - D_0}{D_m + D_0},$$

where D_m is the density of seedlings using the microsite of interest and D_0 is the density of seedlings not using the microsite of interest. This index was used due to its robust statistical properties (Armas et al., 2004) and its previous use in assessing microsite facilitation of seedlings (Redmond & Barger, 2013; Redmond et al., 2018). Density was calculated as the number of seedlings in a certain microsite divided by the available area of that microsite within the belt transect (as measured using the line point-intercept method). Values of *I* range from −1 to +1, with negative values indicating a negative association with the microsite and positive values indicating a positive association. Values close to zero indicate no association. Sites were only analysed if the expected number of seedlings established in the microsite of interest by chance (proportion of microsite in the belt transect × number of aspen seedlings found) equalled or exceeded 0.9. This cut-off was used to ensure that the interaction index reflected the actual association of microsites with seedlings rather than just a lack of availability of that microsite on the belt transect (e.g., Redmond & Barger, 2013). This allowed us to analyse 11 sites for bare soil association, 11 sites for vegetation association, and 10 sites for nurse object association. Bare soil included burned and unburned bare mineral soil with no litter, duff, moss, rock or wood presence, nurse objects included both rocks and CWD greater than the 5-cm diameter, and nearby vegetation included both understory grasses and forbs in this analysis (shrubs were not found near aspen seedlings at any sites). Assumptions of normality were checked for all variables and two-way, one-sample *t*-tests were used to evaluate whether interaction index values for bare soil, vegetation and nurse objects were significantly different than zero ($p < 0.05$).

We expected nurse objects to facilitate seedling establishment more at climatically extreme sites (e.g Conver et al., 2020; Drezner, 2007); therefore, the interaction index for nurse object association at each site was used as a response variable in a multiple regression model (as in Redmond et al., 2018) to investigate the influence of topographic variables on nurse association. The interaction index used here is linear and continuous within its range and is, therefore, safe to use in statistical operations (Armas et al., 2004). Heat load index, elevation and their interaction were considered as predictor variables for the model. Model selection was performed by evaluating AICc of models including all subsets of the predictor variables, using the 'dredge' function in the 'MuMin' package in R (Barton, 2019). The model with the lowest AICc value was selected and used for inference.

3 | RESULTS

3.1 | Disturbance effects on upslope expansion

We found evidence for upslope aspen expansion via aspen seedling establishment; notably, this expansion only occurred in beetle-impacted sites that burned (Figure 2). In total, 80 aspen seedlings were found on 15 upper elevation sites within burned areas. The average seedling density across these sites was 133 (± 24.7 SE) seedlings per hectare. Aspen suckers were encountered only on the pre-fire aspen sites, averaging 4400 (± 1539 SE) suckers per hectare on burned/beetle-impacted sites and 6443 (± 2437 SE) on unburned/beetle-impacted sites. The elevation difference between the pre-fire adult aspen clone at a site and the highest seedling found at that site (local expansion) ranged from 73 to 395 vertical metres (Figure 2). The highest aspen seedling found was at 3678 m on an east-facing slope (see Appendix S4 in Supporting Information), which was 172 m higher than the conservative pre-fire regional elevational limit of 3506 m, and 110 m higher than the more liberally estimated pre-fire regional limit of 3568 m.

Relative to unburned/beetle-impacted sites, burned/beetle-impacted sites above the pre-fire aspen stands had longer distances to nearest live adult aspen (d.f. = 13.2, $t = -3.1$, $p = 0.008$), less canopy (d.f. = 13.6, $t = 2.4$, $p = 0.029$), understory vegetation (d.f. = 13.2, $t = 3.0$, $p = 0.011$), and duff cover (d.f. = 13.6, $t = 3.4$, $p = 0.005$), and more bare soil cover (d.f. = 12.2, $t = -2.4$, $p = 0.03$) (Figure 3). Per cent CWD was not significantly different between burned and unburned beetle-impacted sites ($p > 0.9$). Mean live Engelmann spruce cover, as computed in Savage et al. (2017) for plots with trees, was only 5.2% (± 0.4% SE) in unburned/beetle-impacted sites and averaged 0.8% (± 0.3% SE) in burned/beetle-impacted sites. Percentage of dead trees of all species, as measured in the stand-structure plots, averaged 46.4% (± 0.05% SE) in the unburned/beetle-impacted sites and 95.7% (± 0.02%) in the burned/beetle-impacted sites, while six unburned and three burned beetle-impacted sites contained no trees. All site characteristics were uncorrelated to distance to the fire perimeter, indicating that edge effects likely did not influence the results.

Along the burned elevational transects, upslope aspen expansion (ie, aspen seedling establishment) was associated with CWD and elevation. There were five models with delta AICc values < 2 (see Table S2.1 in Appendix S2), and the model with the lowest AICc included elevational transect as a random intercept and elevation, % CWD and distance to seed source as predictor variables, of which only elevation and % CWD were significant ($p < 0.05$). Elevation was negatively associated with seedling abundance, whereas % CWD positively predicted seedling abundance (Figure 4). Notably, the standard deviation in log-seedling abundance among elevational transects (2.9) was larger than the effects of elevation and % CWD, indicating high spatial variability in seedling abundance.

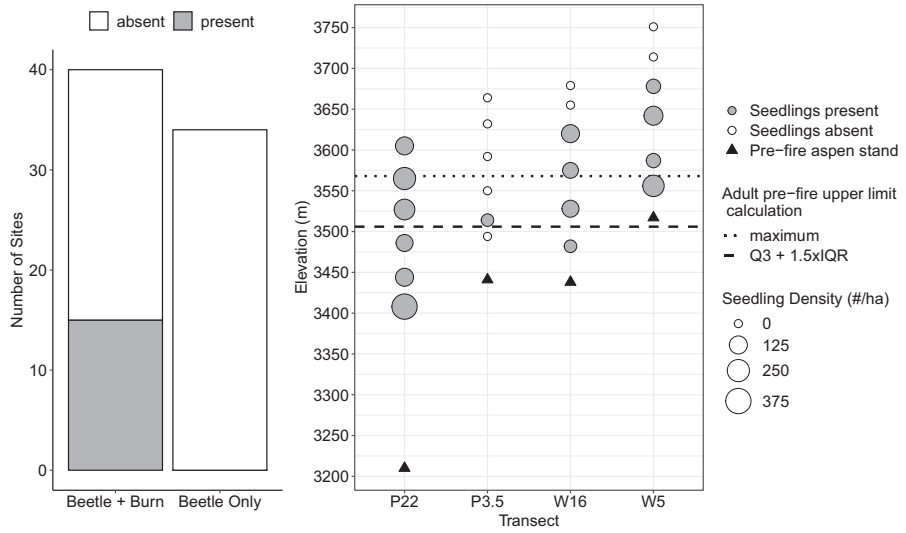

FIGURE 2 Left panel: Number of sites where aspen seedlings were found (grey) versus not found (white) for beetle-impacted and burned vs. beetle-impacted only (unburned) sites in the San Juan Mountains, CO, USA. Right panel: Aspen seedling presence and density (# of seedlings per hectare) at sites surveyed on all elevational transects where aspen seedlings were found. Black triangles represent the pre-fire aspen stands on the elevational transect and the circles represent all sites surveyed on each elevational transect where colour indicates aspen seedling presence (grey) or absence (white) and size indicates the density of aspen seedlings found at each site. Horizontal lines show the two estimates of the pre-fire adult aspen upper limit calculated in the aerial imagery analysis: maximum elevation (dotted) and Q3 + 1.5 × IQR (dashed)

3.2 | Microsite association of aspen seedlings

Aspen seedlings found across all sites occurred under an average canopy density of 6.8% (± 0.67 SE) with an average litter depth of 0.79 cm (± 0.13 SE). Fifty-two per cent of the seedlings were nursed, 70% were within 5 cm of a forb or grass and 76% were browsed. Seedlings showed a positive association with microsites near understory vegetation (mean interaction index ± 1 SE = 0.35 ± 0.15; $t = 2.4$, d.f. = 10, $p = 0.036$), with 9 out of 11 sites analysed having a positive interaction index (Figure 5). Seedlings showed no association with bare soil (mean interaction index ± 1 SE = 0.15 ± 0.17; $t = 0.92$, d.f. = 10, $p = 0.38$; Figure 5).

Association with nurse objects (i.e. logs and rocks) strongly varied among sites (mean interaction index ± 1 SE = 0.16 ± 0.17), and a two-way *t*-test revealed no significant difference from zero ($t = 0.93$, d.f. = 9, $p = 0.38$), indicating that seedlings did not have an overall association with nurse objects (Figure 5). This variability in nurse object association is likely driven by variability in local climatic conditions: both heat load index and elevation were significant predictors of nurse interaction index ($t = -2.7$, $p = 0.029$; $t = 3.2$, $p = 0.014$, respectively) with heat load exhibiting a negative effect and elevation exhibiting a positive effect on nurse interaction index (Figure 6). This implies that nurse objects are more beneficial at high elevation sites and those with less solar radiation at the upper elevational extremes of aspen's range.

4 | DISCUSSION

This study documents disturbance-facilitated range expansion at the leading edge for a widespread wind-dispersed tree of North America and the specific conditions under which expansion is occurring. Aspen seedlings were found above the upper elevational limit of adult aspen across the study area, and only in areas where recent high-severity fire overlapped prior to spruce beetle kill (Figure 2). The results presented here demonstrate that plant species range shifts may be catalysed by some disturbance types, but not others, depending on establishment requirements. Wildfire resulted in low cover of duff, understory vegetation and canopy in these subalpine ecosystems (Figure 3), which likely facilitated aspen seedling establishment. Notably, unburned areas also experienced extensive canopy mortality from a spruce beetle outbreak, but this disturbance alone did not facilitate aspen seedling establishment above its upper elevational limit (Figure 2). Expansion at the leading edge is not only governed by the changing climate but can also be highly localized and dependent on the availability of specific microsite conditions needed for seedling establishment.

4.1 | Keeping pace with climate change

Many studies have documented upward shifts in species optimum elevations due to climate warming, but hardly any tree species have been documented to migrate fast enough to keep pace with climate warming at their leading elevational edge (Lenoir et al., 2008; Lu et al., 2021; Renwick & Rocca, 2015). Migration lags for trees at the leading edge are often attributed to dispersal limitations, lack of suitable habitat, competition and climatic constraints (Renwick & Rocca, 2015). Aspen seedling presence upslope of adult pre-fire stands in this study indicates that these barriers were overcome and that elevational tracking of changes in climate may be possible

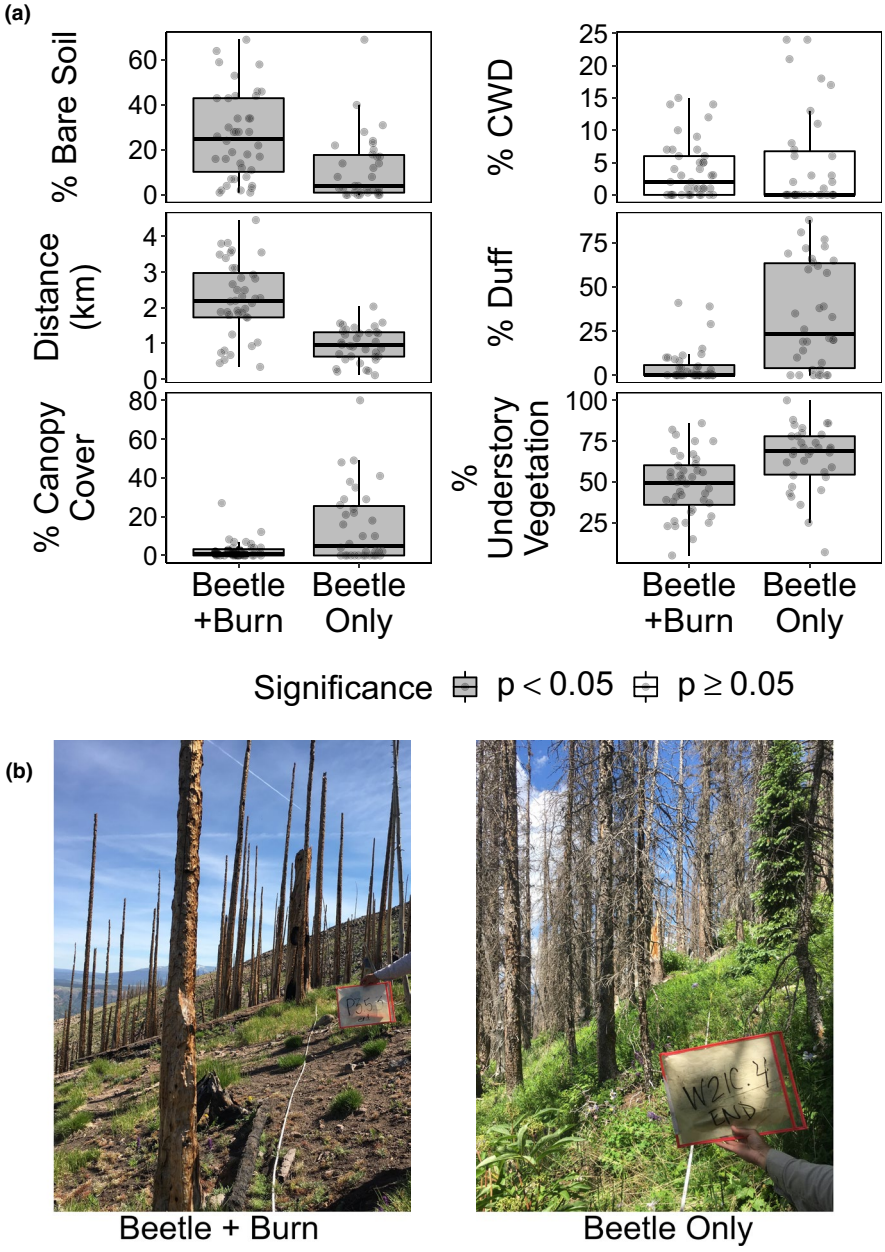

FIGURE 3 Differences in site characteristics between beetle-impacted and burned and beetle-impacted only (unburned) sites in the San Juan Mountains, CO, USA. (a) Box plots shown in grey (% bare soil, distance to the seed source, % duff, % canopy cover and % understory vegetation) are significantly different ($p < 0.05$) between the site types. Boxes bound the first and third quartiles of the data and the horizontal line indicates the median. The vertical lines indicate the lowest and highest observations within 1.5 × IQR (inter-quartile range) of the first and third quartiles. Data for each site is shown in points; 40 burned sites and 34 unburned sites were evaluated. (b) Photograph of a beetle-impacted and burned site (left) and a beetle-impacted only site (right)

for aspen and other disturbance facilitated species under certain conditions. Post-fire dominance of aspen via resprouting has been predicted for sites in the study area where aspen previously existed (Andrus et al., 2021); however, the fact that no suckers were found at sites above the pre-fire aspen stands in this study indicates that in addition to re-establishing dominance after conifer dominance, aspen's realized niche is also expanding. We also found elevation to be a negative predictor of aspen seedling abundance (Figure 4), indicating that the sites surveyed captured the upper elevational limit of aspen's current climate niche. With the reduction of competition and the creation of necessary soil conditions, the West Fork fire complex reduced several barriers to migration. In addition, distance to seed source did not appear to limit aspen seedling establishment; distance to seed source was weakly *positively* associated with aspen seedling establishment (meaning more aspen establishment in areas further from seed sources, Figure 4), which corroborates other studies documenting long-distance dispersal (Landhäusser et al., 2010; Turner et al., 2003). This allowed aspen to expand its range into large burn patches and contrasts with other Rocky Mountain tree species, particularly conifers, for which post-fire regeneration has been repeatedly found to be closely tied to distance to live seed source, with little to no regeneration at distances exceeding 40–400 m (Stevens-Rumann & Morgan, 2019).

The adult aspen stands that make up the pre-fire upper elevational limit in this study represent the highest elevations, and thus coolest climates, where aspen was able to establish in the past. If we conservatively assume these stands established 100 years ago, climate warming in the area would have resulted in at least a 133-m upslope shift of the equivalent climate conditions under which those stands established (temperature decreases at the environmental lapse rate of approximately 6°C with every 1000-m increase in elevation [Baker, 1944] and the average annual temperature has increased 0.8°C in the

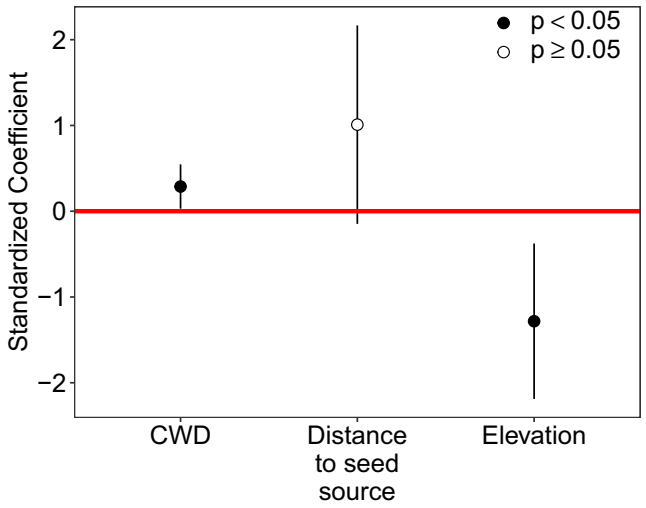

FIGURE 4 Results of the generalized linear mixed model used to assess the effects of site characteristics on aspen seedling abundance in the San Juan Mountains, CO, USA. Points show the standardized coefficient estimate of each fixed effect in the model and lines represent the 95% confidence interval for those effects. The red horizontal line is centred on zero; coefficients with lines that overlap zero are considered non-significant (grey dots), whereas those that do not overlap zero are considered significant (black dots)

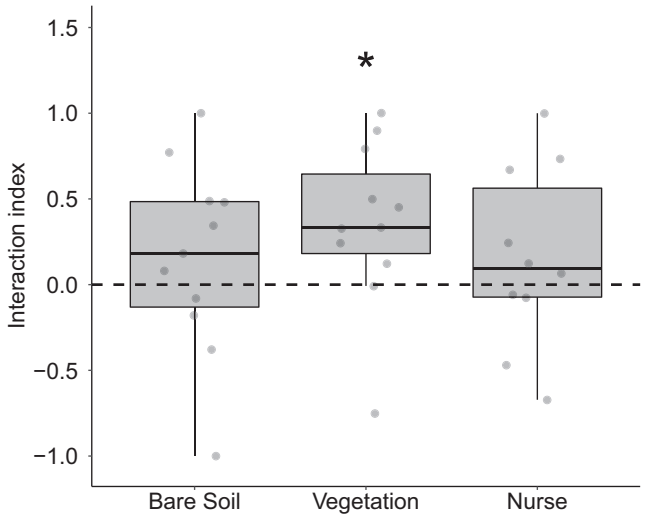

FIGURE 5 Interaction indices between aspen seedlings found in the San Juan Mountains, CO, USA and bare soil, vegetation and nurse objects. Positive interaction indices represent microsites positively associated with aspen seedling establishment, with increasingly positive values representing an increasingly greater association. The dotted horizontal line shows the interaction index value ($I = 0$) that corresponds to no association of the given microsite. Boxes bound the first and third quartiles of the data and the solid horizontal line indicates the median. The vertical lines indicate the lowest and highest observations within 1.5 × IQR (inter-quartile range) of the first and third quartiles. Individual observations are shown as points; there were 11 sites analysed for bare soil and vegetation interactions and 10 sites analysed for nurse object interactions. The asterisk indicates the interaction index was significantly greater than zero ($p < 0.05$)

past century; 0.8 ÷ 6 × 1000 = 133). We found local expansion of 73, 161, 182 and 395 m upward of pre-fire aspen stands and regional expansion of 110–172 m in elevation (Figure 2), suggesting that, following the fire, aspen has expanded upwards in many settings to the extent expected due to climate warming in this region. However, four of the burned and all the unburned elevational transects showed no upslope expansion, indicating that fire is necessary, but not sufficient by itself to accelerate range shifts (suitable microsites are also needed). In their meta-analysis, Renwick and Rocca (2015) found no evidence of any tree species keeping pace with climate change at its leading elevational edge. Regionally, this seems to be the case for aspen as well, considering that much of the landscape is still unburned and that even in burned areas aspen seedling density was relatively low (133 seedlings/hectare on average among sites with seedlings). Aspen may be unique relative to other tree species in its ability to track changes in climate as quickly as they are occurring, though disturbance history and site factors clearly play a large part in range shifts, as discussed in the sections below.

4.2 | Disturbances vary in their impact on species range shifts

Our results suggest that wildfire, but not beetle-kill alone, promotes upward range expansion of aspen and likely other shade-intolerant species with long-distance dispersal capabilities. Insect outbreaks, drought and disease usually cause mortality of only certain tree species and result in moderate increases in understory light conditions and often increased litter layer depth (Astrup et al., 2008; Carlson et al., 2020; DeRose & Long, 2010). These conditions have been shown to promote germination and advanced regeneration of shade-tolerant species that can germinate under dense litter layers (Renwick et al., 2016), and even support aspen suckers (Diskin et al., 2011), but, as shown here, do not appear to facilitate aspen seedling establishment. In contrast, severe wildfire drives greater reductions of canopy cover than insect outbreaks and exposes bare mineral soil, which facilitates the establishment of many shade-intolerant species that rely on high light for germination and growth (Johnstone et al., 2010; Scheller & Mladenoff, 2005) and require bare mineral soil or limited litter for successful establishment (Landhäusser et al., 2010). These two factors (high light and limited litter/duff cover) in burned areas (Figure 3) likely provided the conditions needed for aspen seedling establishment.

Our burned sites also experienced beetle-kill, so we cannot rule out whether the combination of wildfire and beetle kill, or just wildfire alone, was necessary for aspen seedling establishment. Yet, several other studies have documented the fire-facilitated establishment of aspen by seed, making it likely that wildfire was the primary catalyst of this upward range shift (Fairweather et al., 2014; Kreider & Yocom, 2021). Burn severity did not seem to impact aspen seedling abundance in this study as it has in others (Gill et al., 2017) but this is likely because most burned sites experienced near-complete canopy mortality regardless of burn severity, because of prior beetle-kill. Our results

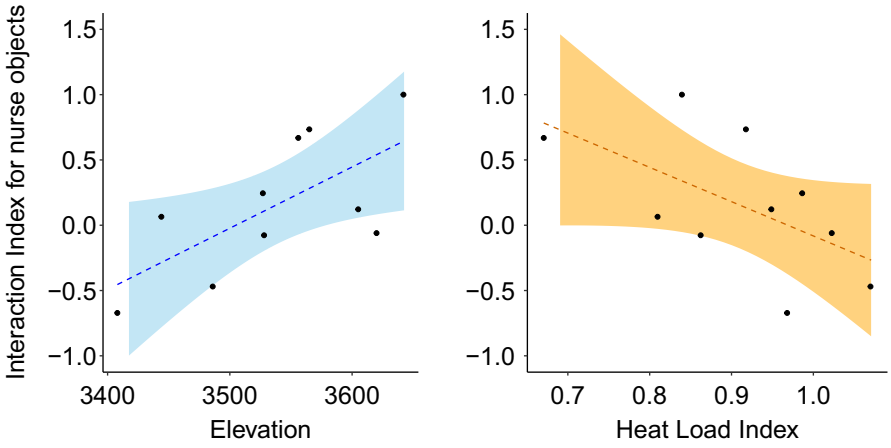

FIGURE 6 The predicted mean effect (shading shows 95% confidence interval) of elevation (left) and heat load index (right) on the interaction index for nurse objects and aspen seedlings in the San Juan Mountains, CO, USA. Closed circles show each data point rather than partial residuals. Both predictors were significant at the $p < 0.05$ level

emphasize that not all disturbance types are equal, supporting other studies documenting the key importance of particular disturbances, such as wildfire and forest harvesting, in facilitating range shifts of shade-intolerant species (Brice et al., 2020; Johnstone & Chapin, 2003; Landhäusser et al., 2010). We occasionally observed aspen seedlings in unburned/beetle-impacted areas while hiking to sites (see Appendix S3); however, this was a rare occurrence compared to burned areas, reflecting the data collected. Thus, regeneration of shade-intolerant species can occur after insect outbreaks, but this disturbance type is unlikely to catalyse range expansion for these species. However, stand-replacing disturbance events can also serve as barriers to migration for species with limited dispersal capabilities (Rayfield et al., 2021; Thom et al., 2017). Thus, spatially extensive disturbances may only be effective at facilitating range shifts among species like aspen with long-distance dispersal capabilities.

4.3 | Range shifts are highly localized

While the results of this study suggest a positive impact of high severity disturbance on range shifts for shade-intolerant species at the leading elevational edge, the patchiness of post-disturbance recovery found here points to the highly localized nature of range shifts across the landscape. Half of the burned elevational transects surveyed experienced no upward migration of aspen via seedlings (Figure 2), despite being equally as near to live seed sources and experiencing similar degrees of warming over the past century. This was likely due in part to the factors found to predict aspen seedling abundance at the site level, such as elevation and CWD (Figure 4). However, other unmeasured factors may have acted as constraints to seedling establishment across the elevational transect such as topography, wind patterns or soil properties. For example, one of the elevational transects where upward migration was not recorded was the only burned elevational transect on a North-facing slope (where temperatures should be cooler), and another had most sites located on excessively rocky terrain (likely to have low soil water holding capacity). This adds support to the growing consensus that predicting range shifts based on bioclimate modelling alone is not sufficient to accurately predict where species will occur in the future. Rather, other topographic, edaphic, biological and stand structure data are needed to better predict where range shifts are likely (Benito Garzón et al., 2019; Bertrand et al., 2012; Brown et al., 2019; Ettinger & HilleRisLambers, 2013; Rehfeldt et al., 2015).

Microsites can also play a large role in governing range expansions, further refining the climate niche a species can expand into. In this study, CWD cover was a positive predictor of seedling abundance (Figure 4) and nurse objects were associated with aspen seedlings at the highest elevations and coolest sites (Figure 6). Nurse objects have been found to support the establishment of plants above their upper elevational limit by providing protection from the high winds and excessive solar radiation at high altitudes, reducing exposure to frost and increasing soil moisture via snowdrift accumulation on top of the objects (Germino et al., 2002; Resler et al., 2005; Smith et al., 2003). These modifications of the abiotic environment likely explain why aspen seedlings at the highest elevations and coolest sites were positively associated with nurse objects. Nurse objects can also promote seedling establishment by protecting seedlings from browsing (Ripple & Larsen, 2001) or simply acting as seed traps (Haussmann et al., 2010). The association between nurse objects and aspen seedling establishment documented here supports prior studies on the importance of nurse objects in facilitating range shifts, especially for species that exist near treeline (Chen et al., 2020; Pyatt et al., 2016). Since high severity fires increase the abundance of nurse objects on the landscape (in the form of downed trees and exposed rocks), they may facilitate range shifts of species to even higher elevations than they would have been able to establish in the absence of such microsites.

4.4 | Seedlings as early signs of range shifts

Here, we interpret the aspen seedling establishment upslope of adult aspen stands as an early indication of a distributional shift. Yet, while seedlings are often used as early indicators of range shifts, their ecological niches can differ significantly from those of adults (Bell et al., 2014; Ettinger & HilleRisLambers, 2013), and thus it is not yet clear whether these aspen seedlings will eventually reach maturity. Browsing by ungulates and defoliation by invertebrates can reduce growth and prevent juveniles of some tree species from reaching canopy dominance,

thereby limiting range expansion (Rogers & Mittanck, 2014; Smith et al., 2016; Van Bogaert et al., 2009). Annual fluctuations in temperature and precipitation in high elevation areas are also likely to determine whether range expansions will persist. The average temperature is often used to predict habitat suitability for species, but extreme events are likely more important for determining seedling survival to maturity and the persistence of the population (Germain & Lutz, 2020). Using seedlings as proxies for future forest composition is helpful for predicting where range shifts may occur, but must be viewed as an early signal and not a guaranteed shift.

5 | CONCLUSIONS

This study documents early evidence for wildfire, but not bark-beetle, catalysed upward expansion of aspen's elevational range limit via seedling establishment. This is a promising sign that other shade-intolerant species with high dispersal capacity may be able to track rapid changes in climate, especially in areas experiencing recent high severity disturbances. Future studies addressing lower elevation limits and the impact of more site-specific factors on establishment will further elucidate how these range shifts will manifest across the landscape and influence future forest composition. The fire was overwhelmingly the most important factor in determining aspen seedling establishment success, but other microsite factors will play a role in determining the specific sites where seedlings can establish and larger patterns in climate and browse pressure will ultimately influence survival and growth into adult stands. As disturbance events become more frequent and severe (Millar & Stephenson, 2015), lags in upslope migrations for some tree species may be overcome.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data is available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.crjdfn348.

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BIOSKETCH

Katie Nigro's research centres on tree species distributional shifts under changing climate and disturbance conditions. This study is part of her PhD work at Colorado State University investigating the potential for future range expansions under different disturbance scenarios in the western US. She and the other authors investigate a range of topics related to post-disturbance regeneration, forest management and climate change impacts on forests of the western United States.

Author contributions: M.D.R. and M.E.R. conceived the ideas; all authors designed the study; K.M.N. collected and analysed the data and led the writing of the manuscript under the mentorship of M.D.R. All authors contributed substantially to revising the manuscript and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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