Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery

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Landscape Ecology

ISSN 0921-2973

Landscape Ecol
DOI 10.1007/s10980-020-01071-z

Springer

Landscape Ecol
https://doi.org/10.1007/s10980-020-01071-z

RESEARCH ARTICLE

Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery

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Received: 6 March 2020 / Accepted: 13 July 2020

Abstract
Context Distance to seed source is often used to estimate seed dispersal—a process needed for post-fire tree recovery. However, distance, especially in mountainous terrain, does not capture pattern or scale-dependent effects controlling seed supply and delivery. Measuring seed source pattern (area and arrangement) could provide insights on how these spatial dynamics shape recovery.

Objectives We tested metrics and investigated how seed source pattern, tree regeneration traits, scale, and terrain interact to shape post-fire tree recovery. Our research questions were: Does seed source pattern outperform distance when modeling tree species presence and regeneration density? If yes, does seed source pattern have scale-dependent or terrain-dependent effects on regeneration density?

Methods We measured seed source pattern at nested spatial extents around 71 plots and related measurements to local post-fire tree recovery. We used generalized linear models to test metrics and visualize scale-dependent and terrain-dependent effects on regeneration density.

Results Distance sufficiently modeled presence, but seed source pattern outperformed distance when modeling regeneration density. Relevant spatial extents and relationships were species-dependent. For wind-dispersed species, regeneration was associated with more seed source area and more complex arrangements, but terrain mediated these relationships. For serotinous and resprouting species, regeneration was associated with less seed source area and less complex arrangements, which are consistent with high-severity burn sites that promote recovery.

Conclusions Seed source pattern supports spatial resilience and interacts with scale and terrain to shape regeneration density. Accounting for these spatial dynamics could help steward forests facing changing fire regimes.

Keywords Mixed conifer forest · Fire · Seed dispersal · Pattern · Terrain · Spatial resilience

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-020-01071-z) contains supplementary material, which is available to authorized users.

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Introduction

Forests in the western United States are facing changing fire regimes due to higher temperatures, earlier spring snowmelt, and longer fire seasons (Dennison et al. 2014; Abatzoglou and Williams 2016; Westerling 2016; Balch et al. 2017). To steward these forests, managers rely on processes (flows of material and energy) that facilitate post-fire tree recovery. One important process is seed dispersal from surviving trees to sites that burned at high severity. In the field, seed dispersal is often estimated using the straight-line distance to nearest seed source or severe-surface burn (Turner et al. 1997; Donato et al. 2016; Harvey et al. 2016; Kemp et al. 2016; Rother and Veblen 2016). However, distance does not capture how seed source pattern (area and arrangement) controls seed supply and delivery. Logically, more seed source area should increase seed supply and arrangements that are more complex should increase seed delivery. For example, complex arrangements tend to have more forest edge, which can interact with wind and increase the likelihood that seeds are dispersed to adjacent clearings (Greene and Johnson 1996; Damschen et al. 2014). Therefore seed source pattern might better estimate seed dispersal (Haire and McGarigal 2010; Coop et al. 2019; Downing et al. 2019), but little is known about its relative merit against distance and how its interactions with scale and terrain govern post-fire tree recovery.

Early lessons on spatial dynamics in post-fire landscapes emerged from the 1988 fires in Yellowstone National Park, Wyoming, United States. During the historic event, fires burned through lodgepole pine (*Pinus contorta* var *latifolia*) forests, which produce closed cones that form aerial seedbanks in the canopy. Fires trigger the aerial seedbanks to open and release their seeds—a regeneration trait called serotiny. As a result, following the 1988 fires, lodgepole pine recovered prolifically (Turner et al. 2003b) and the burn mosaic shaped seedling density. Large crown fire patches contained the highest seedling densities, and seedling density decreased with increasing distance to severe-surface burn (Turner et al. 1997). Over the next 20 years, these lessons were extended to mixed conifer forests, revealing that regeneration density decreased with increasing distance to seed source (Donato et al. 2016; Harvey et al. 2016; Kemp et al. 2016; Rother and Veblen 2016). Consequently, distance metrics are engrained in certain knowledge on spatial dynamics. However, recently percent area of seed source (Tepley et al. 2017), neighborhood burn severity (Haire and McGarigal 2010), and distance-weighted seed source density (Haire and McGarigal 2010; Coop et al. 2019; Downing et al. 2019) were shown to influence regeneration density. These findings suggest that seed source pattern influences seed dispersal, and knowing the scenarios under which pattern should be measured could inform future field studies and management decision-making.

A challenge with measuring pattern is that processes important at one scale are frequently not important or predictive at another (O'Neill 1989; Weins 1989; Turner 2005). Therefore pattern must be measured at relevant scales to account for ecological dynamics and complexity. Determining these scales a priori can be difficult, and is complicated by the fact that relevant scales are often species specific (Addicott et al. 1987; O'Neill 1989). For instance, species-specific scales might emerge in mixed conifer forests because tree species occupy different "regeneration niches" (Rowe 1983). Tree species that are wind-dispersed depend on off-site seeds (Lyon and Stickney 1974) stored in the surrounding landscape for recovery. In contrast, serotinous and resprouting species rely on on-site seeds or surviving propagules that are local (Lyon and Stickney 1974). As a result, seed source pattern might need to be measured at species-specific scales in mixed conifer forests, reflecting the diverse regeneration traits driving post-fire tree recovery.

An additional challenge with measuring pattern is that off-site seeds do not reach a burned site equally. In reality, terrain affects seed dispersal in multi-faceted ways. For example, terrain alters wind dynamics in ways that alter dispersal distances (Katul and Poggi 2012) and directionality (Trakhtenbrot et al. 2014). Terrain also creates locations in landscapes that seeds are less likely to reach (Reader and Buck 1986). Consequently, a burned site might be surrounded with sufficient seed supply, but terrain can impede seed delivery. Therefore it is necessary to incorporate interactions with terrain when estimating seed dispersal—especially when landscape-level factors control seed delivery. Doing so would add to knowledge about interactions among seed source pattern, tree regeneration traits, and scale, providing insights that could help managers account for spatial dynamics and complexity.

We tested metrics and investigated interactions among seed source pattern, tree regeneration traits, scale, and terrain using a natural experiment in the western United States. Our research questions were: Does seed source pattern outperform distance when modeling tree species presence (RQ1) and regeneration density (RQ2)? If yes, does seed source pattern have scale-dependent or terrain-dependent effects on regeneration density (RQ3)? We measured seed source pattern using presence of live trees in post-fire aerial imagery. We expected seed source pattern to outperform distance because seed source pattern accounted for the entire seed supply. For wind-dispersed species, we anticipated that regeneration density would increase with increasing seed source area or arrangement complexity. However, we expected these relationships to occur at spatial extents matching dispersal distances and be sensitive to terrain, given that landscape-level factors control seed delivery. In contrast, we expected on-site seeds and propagules to buffer serotinous and resprouting species against scale-dependent and terrain-dependent effects, allowing them to exhibit less sensitivity.

Methods

Study area

The study area is located in the Gros Ventre Range southeast of Jackson, Wyoming, United States. Mean minimum temperature is − 28 °C in January, while mean maximum temperature is 30 °C in July (SNOTEL, Granite Creek Station (2063 m), 1990–2019). Mean total annual precipitation is 775 mm (SNOTEL, Granite Creek Station (2063 m), 1990–2019). Elevation ranged from 2044 to 2642 m and loam soils were common in recent soil sampling. The Boulder Fire burned 1522 ha in in the year 2000 and established large, high-severity patches (mean patch area = 58 ha, largest patch area = 97 ha). In the year 2010, the Bull Fire burned an additional 2223 ha, leaving behind small, high-severity patches (mean patch area = 0.2 ha, largest patch area = 26 ha) (Fig. 1). Despite contrasting burn mosaics, the fires burned in close proximity, occurring in areas with similar vegetation and geomorphology. As a result, the Boulder and Bull Fires created a natural experiment in which a gradient of seed source patterns are present in a similar geophysical setting. Further, the majority of both fires occurred in the Gros Ventre Wilderness Area, minimizing post-fire management activity.

Forest composition at the Boulder and Bull Fires includes common tree species within mixed conifer forests in the Northern Rockies. Lodgepole pine (*P. contorta* var *latifolia*) stands are common in warm areas, with Douglas fir (*Pseudotsuga menziesii*) and quaking aspen (*Populus tremuloides*) at times dominating the overstory. In cool areas, forests contain a mixture of lodgepole pine, quaking aspen, subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). High elevation areas also contain whitebark pine (*Pinus albicaulis*). Historically, frequent surface fires occurred, as well as infrequent crown fires under extreme weather conditions (Loope and Gruell 1973). In response, tree species have adapted multiple regeneration traits for post-fire recovery. Subalpine fir, Engelmann spruce, and Douglas fir rely on wind dispersal from seed sources (McCaughey et al. 1986). Lodgepole pine produce both non-serotinous and serotinous cones (Lotan 1976), with percentage of serotinous cones decreasing with increasing elevation and fire return interval (Schoennagel et al. 2003). Quaking aspen in the region can regenerate from seed (Turner et al. 2003a), but predominantly resprout from preexisting root structures following a fire event. Together these forests provide a unique opportunity to study three tree regeneration traits (wind-dispersed, serotiny, and resprouting) in one area, offering insights that can be applied to other mixed conifer forests in the western United States.

Study design

We used an extensive point grid to sample across the Boulder and Bull Fires continuously. To do so, we generated a point grid across both fire extents in ArcMap 10.6.1. Each point represented a potential sampling plot for the study. Points were spaced 500 m apart, creating independent sampling plots because wind rarely carries seeds beyond 250 m from their source (McCaughey et al. 1986). Afterward we overlaid the point grid on high-resolution (1 m) aerial images acquired from the National Agricultural Imagery Program (NAIP). We used NAIP images

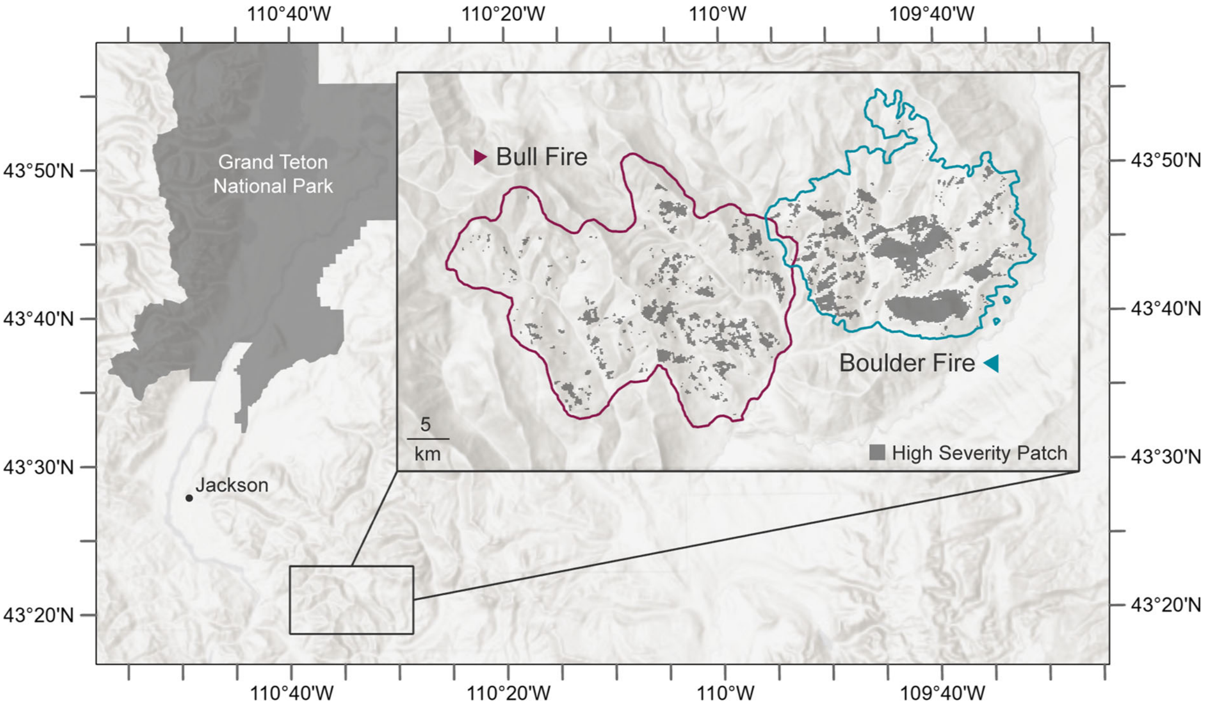


Fig. 1 The Boulder and Bull Fires are located in the Gros Ventre Range southeast of Jackson, Wyoming, United States. Although occurring in close proximity, the Boulder and Bull Fires created divergent spatial patterns of burn severity. As a result, the fires provided a natural experiment to test metrics and investigate the effect of seed source pattern at different spatial extents on post-fire tree recovery. High severity patches characterized where tree mortality was greater than 90%

captured after each fire event, using a 2006 image and a 2012 image for the Boulder and Bull Fire respectively. To answer our research questions, we needed to sample burned plots to measure post-fire tree recovery. Therefore all points were visually inspected and points that appeared unburned were not used in the study.

Field data

We collected field data to measure local post-fire tree recovery. However, due to the rugged terrain, we were unable to visit all potential sampling plots for the study. To prioritize which plots would be sampled, we used non-metric multidimensional scaling (NMDS), the Bray–Curtis dissimilarity metric, and the 'vegan' package (Oksanen et al. 2019) in R version 3.6.1. NMDS collapses data from multiple dimensions into just a few, allowing multivariate data to be plotted, visualized, and then grouped based on similarity. We used NMDS to collapse pattern metrics calculated at the widest radius (250 m) into groups with similar seed source pattern, which we sampled during fieldwork equitably.

We sampled 71 plots across the Boulder and Bull Fires. At each plot, we established 2 × 30 m transects oriented north–south and east–west, in which we counted and identified all tree seedlings (< 1.4 m in height) and saplings (≥ 1.4 m in height and 2.5–12.5 cm DBH). Different cutoffs were used for small (< 1.4 m in height) and mid-size (≥ 1.4 m in height and 2.5–6 cm DBH) quaking aspen stems to better represent stand structure observed at the Boulder and Bull Fires. Together the counts indicated *tree species presence* and *regeneration density* (stems ha^{-1}). We expected to capture the majority of regeneration initiated by fire because most post-fire establishment occurs within 4 years in the Northern Rockies (Harvey et al. 2016). Additionally, we stood at the plot center and recorded *distance to seed source* (m) for each regeneration trait: wind-dispersed (subalpine fir, Engelmann spruce, or Douglas fir), serotiny (lodgepole pine), or resprouting (quaking aspen). We recorded distance to seed source using a laser rangefinder, which can capture distances up to 500 m away. If a seed source was observed beyond 500 m, then its regeneration trait was assigned a distance of 750 m for data analysis. Further, when no seed sources were observed, we assigned the regeneration trait a distance of 1000 m for data analysis.

Geospatial data

We used geospatial data to quantify seed source pattern at nested spatial extents around plots sampled in the study. To do so, we mapped live tree canopy cover using object-based image analyses on the NAIP imagery. All object-based image analyses were completed using Feature Extraction in ENVI 5.5. The object-based image analyses grouped similar pixels into vector objects, which were then classified as "tree" or "no tree" using textural and spectral properties. The "tree" class was our seed source proxy. We validated the final maps using confusion matrices, allowing us to calculate Cohen's Kappa and access accuracy. Given that NAIP images were captured in different years, we generated a confusion matrix for the 2006 image (Kappa = 0.71, accuracy = 85.26%, n = 95) and 2012 image (Kappa = 0.54, accuracy = 76.77%, n = 95) separately. Further, we ground-truthed the final maps in the field (Kappa = 0.82, accuracy = 90.91%, n = 22).

Following map creation, we quantified seed source pattern using the 'landscapemetrics' package (Hesselbarth et al. 2019) in R version 3.6.1. The package includes dozens of landscape metrics that represent different components of pattern, including area, edge, aggregation, or complexity. To determine which metrics would be used to measure seed source pattern, we started with a suite that captured area (percentage of landscape, total area) and arrangement (mean fractal dimension, total edge, edge density, contagion, clumpy, patch cohesion, mean shape index, mean contiguity). Certain metrics were calculated at the class level (structure of "tree" class only) and others at the landscape level (structure of "tree" and "no tree" classes together) to capture different levels of heterogeneity. However, a concern with these metrics is that metrics can be highly correlated, making the information redundant (Ritters et al. 1995). To mediate this concern, we calculated Pearson correlation coefficients to check for multicollinearity. If two metrics were highly correlated ($\geq$ 0.80), then one was removed from the study. At the class level, two metrics remained: *percentage of landscape* (percentage of landscape with seed source; 0 to 100%) and mean *fractal dimension* (seed source arrangement less or more complex; 1.0 to 2.0) (Fig. 2a). Additionally, one metric remained at the landscape level: *contagion* (more complex with classes dispersed/interspersed equally or less complex with one class dominating the landscape exclusively; 0 to 100). For each plot, we calculated these three metrics at nested spatial extents: 25 m, 50 m, 100 m, 150 m, 200 m, 250 m radii (Fig. 3).

We also quantified terrain to incorporate how surrounding topography affects seed delivery. For each potential sampling plot, we identified the highest point along 16 cardinal directions in a pre-determined radius using a digital elevation model (1/3 arc-second) from the USGS 3D Elevation Program and the Relief Visualization Toolbox (Zakšek et al. 2011). The toolbox measured the zenith angle between the plot and each highest point, averaging the 16 zenith angles to calculate *openness* (plot positioned below terrain or plot positioned above terrain; 0 to 180°) (Fig. 2c). Therefore openness quantified a plot's position relative to surrounding terrain, which determines whether a plot is positioned below or above seed sources nearby. Following the nested approach used for seed source pattern, we calculated openness at 50 m, 100 m, 150 m, 200 m, and 250 m radii, respectively. We did not use a 25 m radius because the toolbox calculates openness at 10 m intervals only. Collectively, our geospatial data allowed us to measure surrounding landscape structure at different spatial extents, which we then related to field data collected at the focal plot (Tischendorf and Fahrig 2000).

Data analysis

We created a series of generalized linear models (GLMs) to answer our research questions in the study. All GLMs were built using the 'MASS' package (Venables and Ripley 2002) in R version 3.6.1. To answer RQ1, we used logistic regression to model the probability of tree species presence during post-fire tree recovery. We used the full dataset and modeled one tree species for each regeneration trait, with subalpine fir representing wind-dispersed, lodgepole pine representing serotiny, and quaking aspen representing resprouting. Although lodgepole pine and quaking aspen can also regenerate from wind-

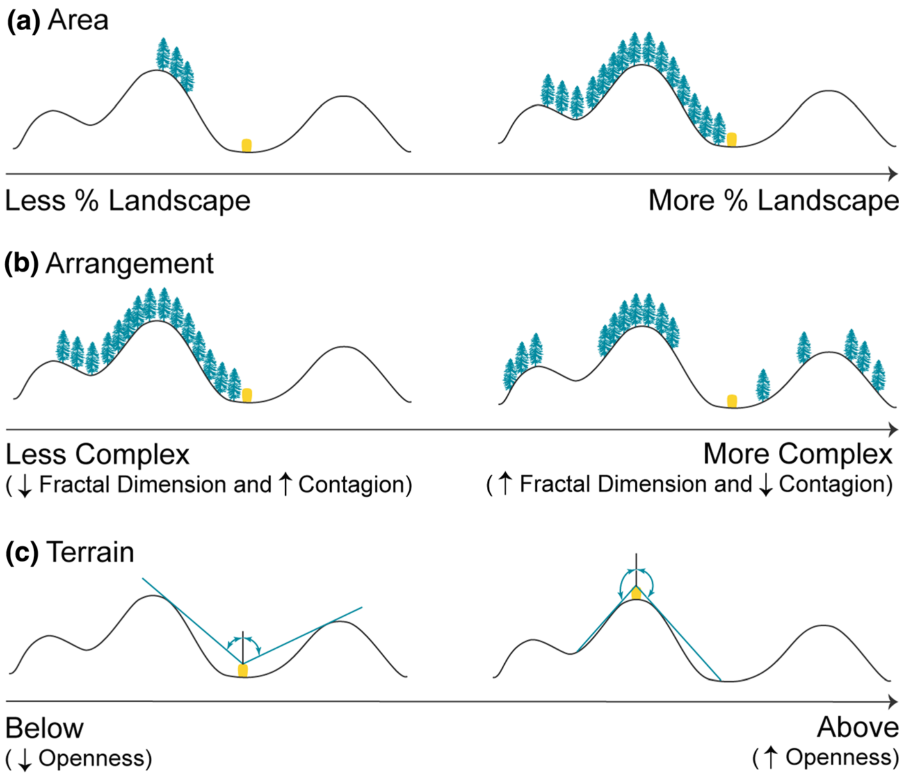


Fig. 2 We used three metrics to measure seed source pattern in the study. Seed source area (**a**) was measured using percentage of landscape and arrangement (**b**) was measured using mean fractal dimension and contagion collectively. We measured both area and arrangement because two sampling plots (illustrated with yellow pins) can be surrounded with the same area or seed supply. However, the arrangement creates different levels of complexity, affecting processes like seed delivery. To measure terrain (**c**), we used an openness metric, which measured zenith angles to determine whether sampling plots were below or above surrounding topography

dispersed seeds, we assigned these tree species to their predominant regeneration trait. To determine whether seed source pattern outperformed distance to seed source, we first created "distance models" for each tree species using the following fixed effects:

$$\log\frac{\mathrm{p_i}}{1-\mathrm{p_i}} = \beta_0 + \beta_1\mathrm{x_{1i}} + \beta_2\mathrm{x_{2i}} + \varepsilon_\mathrm{i}$$

where p_i was probability of tree species presence at plot i, x_{1i} was distance to seed source for the corresponding regeneration trait at plot i, x_{2i} was fire ID for plot i, βs were fixed effect coefficients, and ε_i was the residual at plot i. Next we built "pattern models" for each tree species using the following fixed effects:

$$\log\frac{\mathrm{p_{ij}}}{1-\mathrm{p_{ij}}} = \beta_0 + \beta_1\mathrm{x_{1ij}} + \beta_2\mathrm{x_{2ij}} + \beta_3\mathrm{x_{3ij}} + \beta_4\mathrm{x_{4i}} + \beta_5\mathrm{x_{5i}} + \varepsilon_\mathrm{ij}$$

where p_{ij} was probability of tree species presence at plot i for spatial extent j, x_{1ij} was percentage of landscape at plot i within spatial extent j, x_{2ij} was mean fractal dimension at plot i within spatial extent j, x_{3ij} was contagion at plot i within spatial extent j, x_{4i} was openness at plot i, x_{5i} was fire ID for plot i, βs were fixed effect coefficients, and ε_{ij} was the residual at plot i for spatial extent j. We tried all combinations of fixed effects and their interactions, calculating the AIC for each combination separately. Additionally, we checked for uninformative variables to confirm that all fixed effects were related to the response variable (Leroux 2019). To reduce the number of potential combinations, we only included openness at a single spatial extent – the one most correlated with the probability of tree species presence. We included fire ID as a fixed effect because time since fire and post-fire

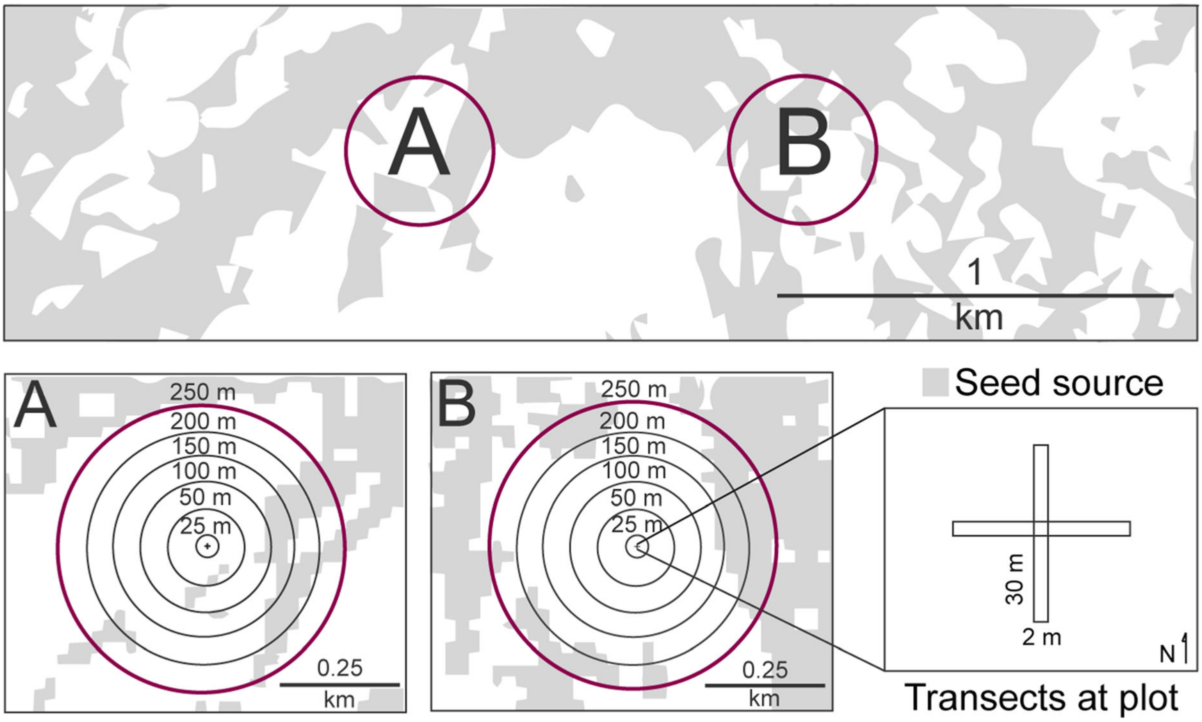


Fig. 3 We measured seed source area and arrangement around plots at nested spatial extents: 25 m, 50 m, 100 m, 150 m, 200 m, and 250 m radii. In the field, we used transects at each plot to record tree species presence and regeneration density. We then related seed source pattern to the field data, allowing us to test the effect of pattern at different spatial extents on post-fire tree recovery

climate varied between the Bull and Boulder Fires. If fire ID was insignificant, then we assumed these differences did not influence post-fire tree recovery.

Following model building, we compared ΔAICs to determine whether seed source pattern outperformed distance. To reduce the number of models, we grouped together distance models and 4 pattern models from each spatial extent, comparing a total of 26 models for each tree species respectively. Pattern models with the lowest AICs were selected for the group. We then calculated ΔAIC using the following equation:

$$\Delta \mathrm{AIC_i} = \mathrm{AIC_i} - \mathrm{minAIC}$$

where ΔAIC_i was difference in AIC with respect to minAIC for model i, AIC_i was the AIC for model i, and *minAIC* was the minimum AIC in the group. A ΔAIC of 0 indicated the best model in the group, which we corroborated using Akaike weights (Wagenmakers and Farrel 2004). However, alternative models were competitive with the best model if $\Delta\mathrm{AIC} < 2$. As a result, we concluded that seed source pattern outperformed distance if no distance models had a $\Delta\mathrm{AIC} < 2$.

To answer RQ2, we used negative binomial regression to model regeneration density. Negative binomial regression is commonly used for ecological count data, given that it addresses challenges associated with overdispersion resulting from spatiotemporal heterogeneity. An additional challenge with ecological count data is zero-inflation, which occurs when more zeroes exist than expected from a negative binomial distribution. To address zero-inflation, we used data subsets that included plots where regeneration was observed for subalpine fir, lodgepole pine, and quaking aspen respectively. From these data subsets, we built and compared distance and pattern models using the same fixed effects from the logistic regression analysis. However, we changed the response variable to regeneration density. Repeating this approach with a different response variable allowed us to account for uncertainty about whether seed source pattern affected presence, density, or both in the study.

To answer RQ3, we used predicted values to better understand pattern models from RQ2. We analyzed pattern models where ΔAIC was < 2, using various levels of fixed effects to predict regeneration density. For the various levels, we used 100 points between the fixed effect's minimum and maximum observation in the study. If a pattern model contained multiple fixed effects, then we varied one fixed effect while holding others at their mean to observe how individual metrics affected regeneration density. Each fixed effect was given a chance to vary. After all predicted values were calculated, we plotted fixed effects against predicted values to visualize relationships between individual metrics and regeneration density. We repeated this approach on the equivalent pattern model at remaining spatial extents, allowing us to observe scale-dependent effects on regeneration density. Additionally, pattern models containing openness as a fixed effect were visualized with contour plots to assess terrain-dependent effects on regeneration density. To reduce the number of pattern models analyzed, we selected a maximum of two pattern models for each tree species – both contained significant coefficients ($p < 0.05$) only and captured the widest range of fixed effects collectively.

Results

We sampled 71 plots across a gradient of seed source pattern during the study (Online Resource 1). For wind-dispersed species, we recorded subalpine fir, Engelmann spruce, and Douglas fir seedlings or saplings in 30, 8, and 12 plots respectively. Lodgepole pine seedlings or saplings were noted in 28 plots and both serotinous and non-serotinous cones were observed on surviving trees nearby. Quaking aspen resprouts were observed in 31 plots. When tree species were present, we observed wide variation in regeneration density (Fig. 4). Mean densities for subalpine fir, Engelmann spruce, and Douglas fir were 610, 408, and 258 stems ha^{-1} respectively. Lodgepole pine was 1692 stems ha^{-1}, while quaking aspen was 1190 stems ha^{-1}. We found a total of 4 whitebark pine seedlings in 2 plots during the study.

When modeling tree species presence, only distance models had ΔAIC < 2 (Fig. 5a). Compared to pattern models, Akaike weights revealed that distance models were at least 8 times more likely to be the best model. For all distance models, distance to seed source was a significant coefficient and negatively related to the probability of a tree species occurring. Fire ID was a fixed effect in certain distance models with ΔAIC $<$ 2. However, fire ID was an uninformative variable with no relationship to tree species presence.

When modeling regeneration density, only pattern models had ΔAIC < 2 (Fig. 5b). However, the spatial extents at which ΔAIC < 2 occurred were species-dependent. For subalpine fir, all pattern models at 50 m and 100 m had ΔAIC < 2. At these spatial extents, percentage of landscape, fractal dimension, and openness were significant coefficients. Pattern models at 150 m and 250 m also had ΔAIC < 2. However, these models were not better than the most competitive distance model, which suggested that seed source pattern at broader spatial extents did not outperform distance. In contrast, pattern models were relevant for lodgepole pine and quaking aspen at 25 m. At 25 m, lodgepole pine had percentage of landscape, contagion, and openness as significant coefficients, while quaking aspen had percentage of landscape and contagion only.

For subalpine fir, analyzing pattern models revealed scale-dependent and terrain-dependent relationships between seed source pattern and regeneration density. Percentage of landscape had a positive relationship with regeneration density (Fig. 6a). The slope of the positive relationship changed across spatial extents, with the greatest slope at 100 m specifically. Fractal dimension also had a scale-dependent, positive relationship with regeneration density. Once again, the greatest slope occurred at 100 m during modeling. However, at 100 m, terrain mediated the relationship between fractal dimension and subalpine fir regeneration density. Predicted values showed that high fractal dimension and low openness supported the highest subalpine fir regeneration density (Fig. 7).

Lodgepole pine and quaking aspen showed only scale-dependent associations between seed source pattern and regeneration density. For lodgepole pine, at 25 m and 50 m, percentage of landscape had a negative relationship with regeneration density (Fig. 6b). However, at broader spatial extents, percentage of landscape was positively related to lodgepole pine regeneration density. For quaking aspen, across all spatial extents, contagion had a positive

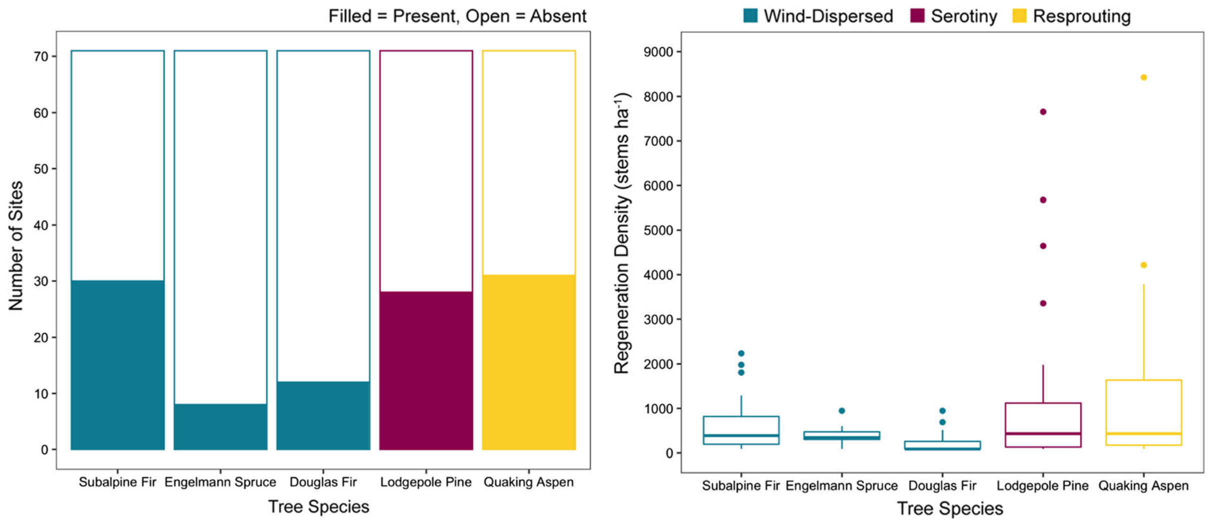


Fig. 4 We sampled a total of 71 plots at the Boulder and Bull Fires. Graphs show the number of plots where tree species were present and their distributions in regeneration density. Tree species are grouped by their predominant regeneration trait (wind-dispersed, serotiny, or resprouting). In addition to these findings, we found a total of 4 whitebark pine seedlings in 2 plots during the study

relationship with regeneration density (Fig. 6c). In contrast, percentage of landscape was negatively related to quaking aspen regeneration density.

Discussion

Our findings provide insights into the influence of landscape-level factors on post-fire tree recovery. We found that distance sufficiently estimated presence, but seed source pattern was better at estimating regeneration density. These associations suggest that distance captures whether seeds reach a site and establish presence, while area and arrangement approximate the number of seeds and ultimately density. Alternatively, associations between seed source pattern and density might reflect how landscape-level and local factors govern different processes during post-fire tree recovery. For example, area and arrangement influence propagule pressure, while local factors (elevation, water deficit) determine local site suitability. If local factors are suitable for tree establishment, then seed source pattern and related seed dispersal processes become important—ultimately shaping regeneration density. Given that local factors are interacting or changing with the warming climate (Rother et al. 2015; Hansen and Turner 2019), estimating both landscape-level and local factors could be critical for predicting forest resilience to fire activity.

Our findings can guide how to estimate seed dispersal when anticipating forest resilience after a fire event. Resilience describes the capacity of a system to “spring back” after a disturbance event to its original composition, structure, or function (Walker et al. 2004). Resilience is challenging to quantify, but defining the resilience of *what* to *what* and accounting for scale are good starting points (Carpenter et al. 2011). When anticipating resilience of *forest composition* to *fire* at the stand-level over successional cycles, our findings suggest that measuring distance to seed source works sufficiently. If anticipating resilience of *forest structure* to *fire*, then measuring seed source area and arrangement is needed given associations with regeneration density. However, seed source area and arrangement must be measured at relevant spatial extents that reflect predominant regeneration traits.

For subalpine fir, seed source area and arrangement are relevant at 50 m and 100 m, matching known wind dispersal distances (McCaughey et al. 1986) for seed delivery. These scales of influence are comparable to those found in pondersa pine (*Pinus ponderosa*) forests (100 or 150 m; Haire and McGarigal 2010), though others found much larger spatial extents to be influential (300 m; Coop et al. 2019). At relevant spatial extents, subalpine fir regeneration increases with increasing seed source area, reinforcing that the total seed source (not just the nearest seed source) influences regeneration density. Additionally, terrain matters at 100 m, as burned sites located below seed source with complex arrangements support the highest subalpine fir regeneration density. In contrast, burned sites positioned above similar arrangements might have a fivefold reduction in regeneration density. Accounting for these spatial dynamics in post-fire landscapes is needed because under benign or moderate fire weather, complex terrain can protect off-site seed sources (Román-Cuesta et al. 2009; Krawchuk et al. 2016; Tepley et al. 2017). But complex terrain also produces locations where off-site seeds are less likely to reach, potentially creating a double-edged sword for post-fire tree recovery.

Fig. 6 Seed source area and arrangement had scale-dependent ▶ effects on subalpine fir (**a**), lodgepole pine (**b**), and quaking aspen (**c**) recovery. Graphs show predicted regeneration densities (shaded areas reflect 95% confidence intervals) across levels of area and arrangement respectively. Brackets group together fixed effects used in the same pattern model. Asterisks indicate the fixed effect had a significant coefficient at that spatial extent ($p < 0.05$). Here we showcased a subset of spatial extents, but findings for all spatial extents are available in Online Resource 3

For lodgepole pine and quaking aspen, seed source area and arrangement are relevant at 25 m, underscoring the ways fire triggers on-site materials to facilitate recovery. At 25 m, lodgepole pine regeneration increases with decreasing seed source area and arrangement complexity. Most likely the absence of seed source is a signal for burn severity. High severity fires reduce live tree canopy cover (our proxy for seed source), but trigger on-site serotinous cones to open (Lotan 1976). As a result, lodgepole pine can recover

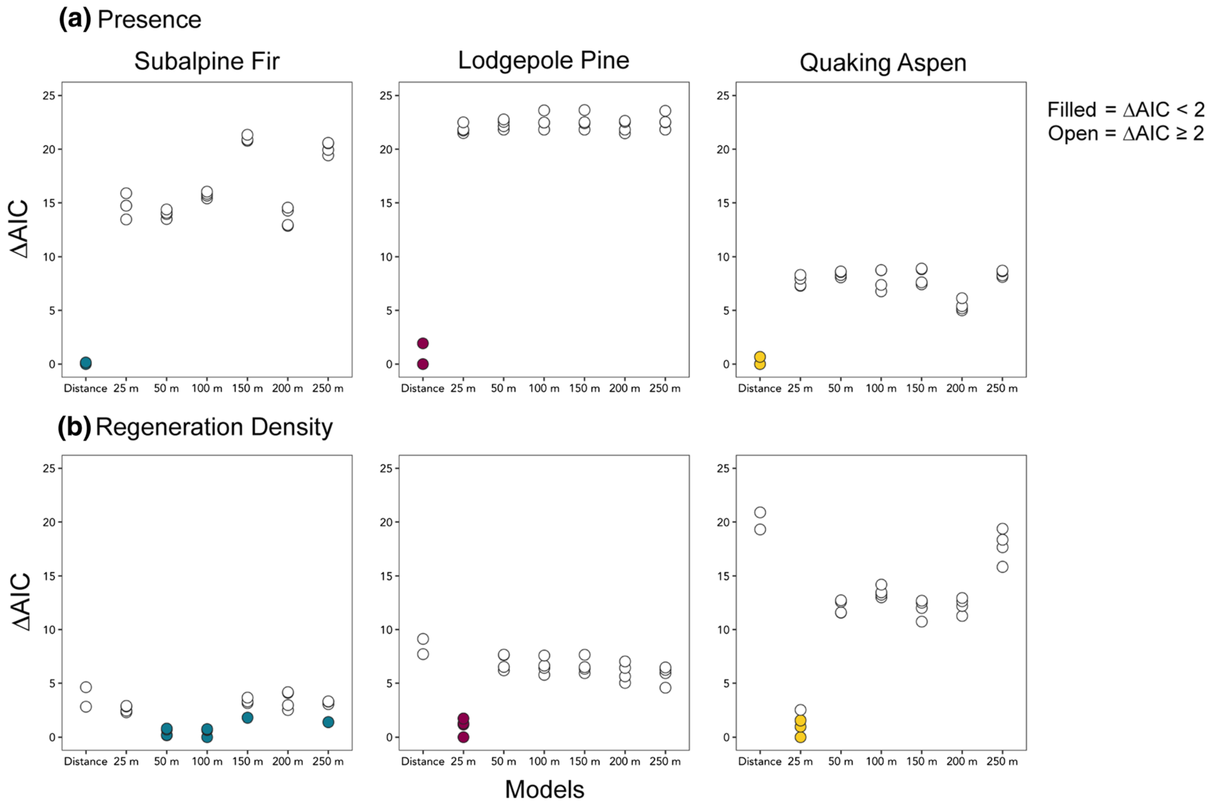
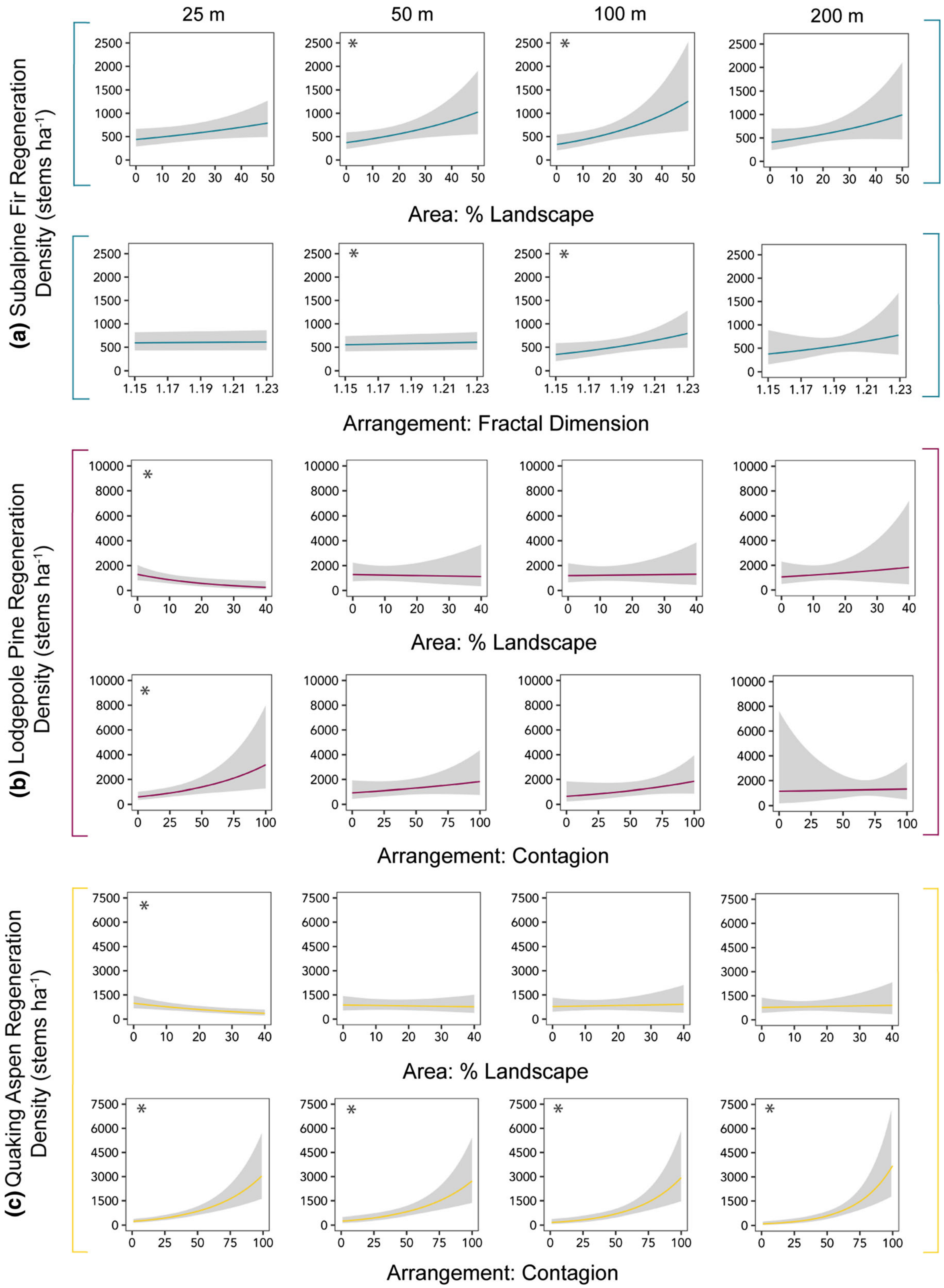


Fig. 5 Distance models were best ($\Delta AIC < 2$) when modeling tree species presence (**a**) during post-fire recovery. In contrast, pattern models were best when modeling regeneration density (**b**), but at which spatial extent was species dependent. On each graph, the first column plots ΔAIC for distance models, while remaining columns plot ΔAIC for pattern models at each spatial extent (25 m, 50 m, 100 m, 150 m, 200 m, and 250 m radii). More details on the distance and pattern models (fixed effects, coefficients, Akaike weights, pseudo R-squareds) are available in Online Resource 2


25 m
50 m
100 m
200 m
(a) Subalpine Fir Regeneration Density (stems ha^{-1})
2500
2000
1500
1000
500
0
0 10 20 30 40 50
Area: % Landscape
1.15 1.17 1.19 1.21 1.23
Arrangement: Fractal Dimension
(b) Lodgepole Pine Regeneration Density (stems ha^{-1})
10000
8000
6000
4000
2000
0
0 10 20 30 40
Area: % Landscape
0 25 50 75 100
Arrangement: Contagion
(c) Quaking Aspen Regeneration Density (stems ha^{-1})
7500
6000
4500
3000
1500
0
0 10 20 30 40
Area: % Landscape
0 25 50 75 100
Arrangement: Contagion
*

prolifically after burning at high severity. Short fire-return intervals can reduce this regenerative capacity (Buma et al. 2013; Hansen et al. 2018; Turner et al. 2019), but there was no evidence of this constraint in the study. Similarly, at 25 m, quaking aspen regeneration increases with decreasing seed source area and arrangement complexity. Given that quaking aspen resprouts from on-site root structures following stand-replacing fire, the absence of seed source might again be a signal for burn severity. If so, these trends would be congruent with lodgepole pine, reinforcing that homogenous, stand-replacing fires are associated with recovery. For both tree species, we did not observe terrain-dependent effects, suggesting that on-site seeds and propagules buffer against topography.

Measuring seed source area and arrangement might compliment other approaches commonly used to estimate seed dispersal during post-fire tree recovery. For example, dispersal kernels are often used to model seed rain from an individual tree to its surroundings. To scale up from the individual to landscape level, distance-weighted metrics total the kernel-based seed contributions (Tautenhahn et al. 2016; Landesmann and Morals 2018) or seed source presence (Haire and McGarigal 2010; Coop et al. 2019; Downing et al. 2019) of all pixels within a pre-determined radius from the focal point. However, using metrics grounded in dispersal kernels requires assumptions on kernel shape and scale parameters (Clark et al. 1999; Greene et al. 2004). Additionally, assumptions must be made on how terrain affects those parameters (Katul and Poggi 2012). Measuring seed source area and arrangement using landscape metrics removes the need for these assumptions when linking seed source pattern to regeneration density. However, future work is needed to identify synergies among approaches with varying levels of mechanistic detail and complexity.

Given the limitations in our approach, we suggest several future directions for studying and managing forest recovery across heterogeneous landscapes. Although local factors such as elevation (Rother and Veblen 2016), aspect (Donato et al. 2016; Rother and Veblen 2016; Hansen and Turner 2019), and water deficit (Harvey et al. 2016; Stevens-Rumann et al. 2017; Tepley et al. 2017) affect regeneration, our findings suggest the importance of landscape-level factors. By identifying relevant metrics and spatial extents, we isolated how the spatial characteristics of landscape structure influence post-fire tree recovery. However, including local factors in future work would provide deeper insights on contexts in which local versus landscape processes shape tree species presence and regeneration density. In addition, future work could test how seed source area and arrangement influence spatial dynamics across broader landscape gradients, perhaps by leveraging datasets (e.g. Coop et al. 2019; Downing et al. 2019) that measured seed sources using similar workflows with NAIP imagery (Walker et al. 2019). A meta-analysis on these datasets would assess the generalizability of our findings across different biophysical landscapes. Finally, terrain affects tree regeneration through interactive processes that include creating favorable microclimates for establishment (Dobrowski 2011) and influencing wind dynamics that control dispersal (Trakhtenbrot et al. 2014). We aimed to capture the latter process, but an experimental approach isolating the two processes is needed to determine the root of terrain-dependent effects in the study. Doing so in future work would add to understanding the relative influence of different processes on post-fire tree recovery.

While identifying future areas of research, our findings highlight ways seed source pattern could support forest resilience to changing fire regimes. Fire spatial patterns are changing (Stevens et al. 2017) and leaving behind complex mosaics of surviving trees (Halofsky et al. 2011; Collins et al. 2017). Ecologically, these mosaics sustain important functions (Meddens et al. 2018) and their spatial characteristics

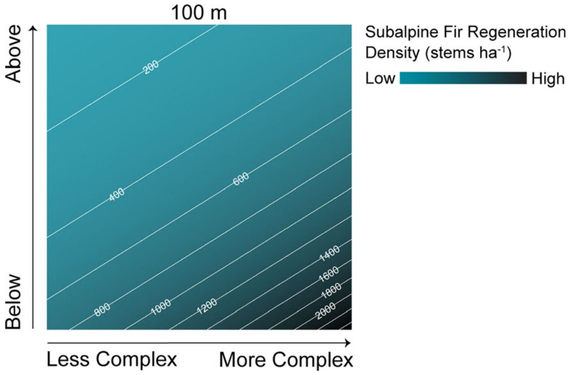


Fig. 7 For subalpine fir, terrain mediated relationships between seed source arrangement and regeneration density. Specifically, we observed terrain-dependent effects at 100 m spatial extents, where plots positioned below more complex arrangements supported the highest subalpine fir regeneration density. Numbers along the white contours show predicted values for subalpine fir regeneration density

might confer spatial resilience (Cumming 2011; Cumming et al. 2017) during recovery. At the stand-level, our findings reinforce that resilience must be considered to have a spatial context governing the flows of materials to a given location (Cumming et al. 2017). As fires grow larger and more severe, robust tree regeneration will be needed to prevent shifts in forest structure that result in the loss of ecosystem services to society. Accordingly, seed source pattern will be influential, even scaling up to support resilient landscapes (Coop et al. 2019) and their regenerative capacity.

Our findings also inform recommendations for managers in the western United States. In this changing world, managers are charged with stewarding resilient landscapes (Wildland Fire Leadership Council 2014). Additionally, federal law requires managers to devote resources to burned sites that are not restocking naturally. To meet these two objectives, placing burned sites in the context of their surrounding seed source pattern could be fundamental to decision-making. It could also help prioritize which burned sites to devote effort, time, and money. Overall our findings suggest that accounting for seed source area and arrangement is needed when anticipating future forest structure and regeneration density. However, managers must be mindful of the spatial extent used during measurements, given that relationships were species-dependent in the study. For subalpine fir, appropriate spatial extents include 50 m or 100 m, while 25 m should be used to anticipate lodgepole pine and quaking aspen regeneration density. For wind-dispersed species, managers must also consider terrain when anticipating regeneration density. Even though a burned site might be surrounded with sufficient seed source, its position in the landscape can impede recovery. Specifically, burned sites positioned above surrounding seed source are most at risk of not restocking naturally. Finding avenues to better incorporate these interactions among seed source pattern, tree regeneration traits, scale, and terrain into spatial planning will be needed as forests in mountainous terrain face changing fire regimes.

Acknowledgements The National Science Foundation (BCS-1901630), Joint Fire Science Program (1910144), National Geographic, National Aeronautics and Space Administration Pennsylvania Space Grant Consortium, and Penn State Center for Landscape Dynamics funded the study. We thank Hunter Mitchell and Shaina Walker for their hard work in the field, as well as Shelby Duncan for their assistance with the object based image analysis. We also thank Diane Abendroth and Bridger-Teton National Forest for their logistical support and permitting the study. Laura Leites, Doug Miller, and Alan Taylor served on JLP's dissertation committee and provided helpful feedback on the manuscript and study.

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