FINAL REPORT

Title: Scale-dependent effects of landscape context on post-fire forest regeneration in the Northern Rockies

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Abbreviations

NAIP .... National Agricultural Imagery Program

Keywords

Fire, conifer forest, fire, seed dispersal, pattern, scale, terrain, resilience

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Abstract

We live in a changing world where climate change, built-up fuels, and human ignitions are causing fires to increase in size, frequency, and severity. In this changing world, managers are charged with stewarding resilient landscapes under the National Cohesive Wildland Fire Management Strategy. Additionally, federal law requires managers to devote resources to burned sites that are not restocking naturally. To meet these goals, accounting for a burned site's surrounding landscape context (defined here as area and arrangement of nearby seed sources) could be fundamental to anticipating its resiliency and whether it restocks naturally. However, little is known about how landscape context interacts with scale, regeneration traits, terrain, and local site conditions to govern post-fire tree recovery. To address these knowledge gaps, we used field data, geospatial data, and statistical models to unravel spatial dynamics playing out across heterogenous post-fire environments. We found that seed source area and arrangement must be measured at relevant spatial extents that reflect regeneration traits. For wind-dispersed species, regeneration was associated with more seed source area and more complex arrangements at 50 m and 100 m spatial extents, but terrain mediated the relationships. For serotinous and resprouting species, regeneration was associated with less seed source area and less complex arrangements at 25 m, which was consistent with high severity fires that promote recovery. Additionally, we found that surrounding seed source area was more important than local site conditions in shaping subalpine fir presence and stocking density. But different thresholds occurred. Specifically, subalpine fir presence required 10% seed source area, while stocking density required 40%. Conversely, local factors like soil nutrients were associated with lodgepole pine presence – underscoring the effects of different regeneration traits. Overall, our findings provide considerations and thresholds to guide managers in better incorporating landscape context in their decision-making.

Objectives

The JFSP GRIN Award supplemented dissertation work on fire, spatial dynamics, and resilience in western United States forests. Accordingly, it contained two objectives:

Objective 1: At what spatial extents do tree species with different regeneration traits respond to landscape context?

In the field, straight-line distance to nearest seed source is often used to estimate the role of seed dispersal in post-fire tree recovery. Accounting for landscape context (defined here as area and arrangement of nearby seed sources) might better capture how all seed sources shape seed dispersal. However, a knowledge gap exists on what spatial extents best capture landscape context, which likely differs among regeneration traits (wind-dispersed, serotiny, or resprouting). We expected relevant spatial extents for wind-dispersed tree species to match dispersal distances, given that landscape-level factors control seed delivery. In contrast, we expected predominantly serotinous and resprouting species to be buffered against scale-dependent effects, given that on-site seeds and propagules exhibit less sensitivity.

Objective 2: What is the relative influence of landscape context and local site conditions on post-fire tree regeneration?

Local site conditions such as water availability, soil nutrients, and ground cover influence tree establishment after fire. However, these local site conditions are rarely considered alongside landscape context when anticipating post-fire tree regeneration – creating a knowledge gap in understanding spatial dynamics that shape whether a burned site will restock naturally. We expected the relative influence of landscape context to be linked to local water availability. For instance, we anticipated that landscape context would be more influential on cooler, wetter northeast aspects because these sites are less constrained by water availability. When landscape context was important, we expected to observe different thresholds for tree species presence and stocking density. We anticipated different thresholds because achieving tree species presence requires fewer seeds from the surrounding landscape than reaching stocking density.

Background

A new fire era in the United States poses significant forest management challenges and costs to society. Due to climate change, built-up fuels, and human ignitions, fires are increasing in size, frequency, and severity. As a result, the western United States continues to endure record-breaking fire years. 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 (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 area and arrangement controls seed supply and delivery (**Figure 1**). Therefore, landscape context 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, regeneration traits, terrain, and local site conditions govern post-fire tree recovery.

A challenge with quantifying landscape context is that processes important at one scale are frequently not important or predictive at another (Weins 1989; O'Neill 1989; Turner 2005). Therefore, area and arrangement 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, landscape context 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 landscape context is that off-site seeds do not reach a burned site equally. 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). As a result, a burned site might be surrounded with sufficient seed supply, but terrain can impede seed delivery. Consequently, 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 landscape context, tree regeneration traits, and scale, providing insights that could help managers better account for spatial dynamics and complexity.

Figure 1. When an individual fire burns across the landscape, it creates substantial spatial variability. Specifically, it leaves behind patches of unburned, scorched, or fire-killed trees that affects distribution of surviving trees and seed supply. Mountainous terrain also creates spatial variability that affects seed delivery.

Even if landscape context supports seeds reaching burned sites, tree establishment may not occur due to local site conditions. For instance, reduced water availability from decreased snowpack and prolonged droughts can constrain tree establishment and ultimately facilitate fire-catalyzed tree loss. In addition to water availability, tree establishment benefits from soil nutrients like nitrogen – a building block for proteins and amino acids required for growth. Finally, ground cover from grasses, forbs, shrubs, and coarse woody debris can ameliorate harsh conditions from increased sun insolation after fire – offering protection to tree seedlings and creating heterogeneity in soil nutrient availability (Hart et al. 2005; Metzger et al. 2008). Collectively, local site conditions are rarely considered alongside landscape context, which could help managers better account for spatial dynamics that determine whether a burned site will restock naturally.

Materials and Methods

Study area

The study area was in the Gros Ventre Range southeast of Jackson, Wyoming, United States (**Figure 2**). The Boulder Fire burned 1,522 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 2,223 ha, leaving behind small, high-severity patches (mean patch area = 0.2 ha, largest patch area = 26 ha). 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, both fires occurred in the Gros Ventre Wilderness Area, minimizing post-fire management activity.

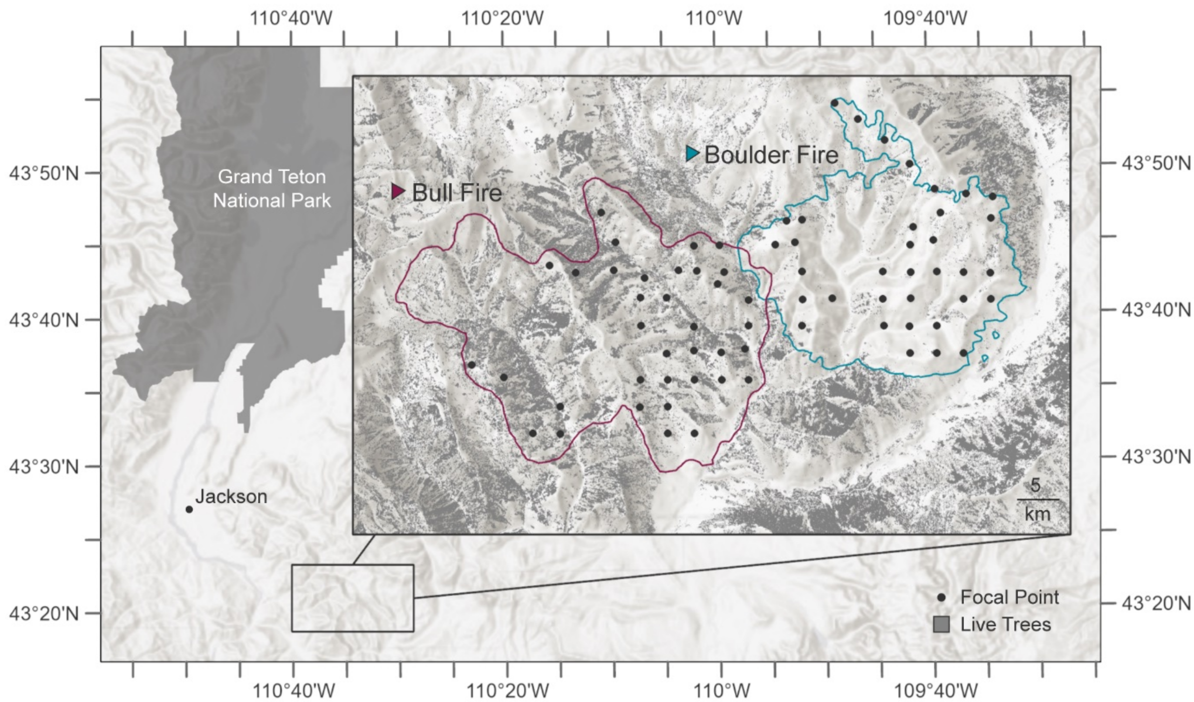

Figure 2. The Boulder and Bull Fires occurred in the Gros Ventre Range southeast of Jackson, Wyoming, United States. With divergent spatial patterns of burn severity, the fires created a gradient of live trees that provide seed source proxies. The gradient spanned areas with similar vegetation and terrain, creating a natural experiment to investigate the relative influence of local and landscape factors on post-fire tree recovery.

Forest composition at the Boulder and Bull Fires includes common tree species within mixed conifer forests in the Northern Rockies. Collectively, these tree species have adapted multiple regeneration traits for post-fire recovery. Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga menziesii*) rely on wind dispersal from seed sources (McCaughey et al. 1986). Lodgepole pine (*Pinus contorta* var *latifolia*) 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 (*Populus tremuloides*) in the region can regenerate from seed (Turner et al. 2003), but predominantly resprout from preexisting root structures following a fire event. Together these forests provided 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 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 captured after each fire event, using a 2006 image and a 2012 image for the Boulder and Bull Fire respectively. To meet our objectives, 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 sampled 71 plots across the Boulder and Bull Fires. At each plot, we established 2x30 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. Afterwards we used the counts to determine *tree species presence*, *regeneration density*, and *stocking density* (>400 conifer stems acre^{-1}). To determine whether plots were stocked or unstocked, we used desired stocking levels in the Forest Plan for Bridger-Teton National Forest (United States Forest Service 2015). 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).

To compare the utility of landscape context against distance to nearest seed source, we stood at the plot center and recorded *distance to nearest 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 nearest 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 1,000 m for data analysis.

We collected additional field data to relate local site conditions to post-fire tree recovery. At the plot center, *elevation* (m), *aspect* (°), and *slope* (°) were measured using a Garmin eTrex 20X, compass, and clinometer respectively. Aspect was transformed using a cosine transformation (Beers et al. 1966), creating an index from southwest-facing plots at 0 to northeast-facing plots at 2. Along each transect, we placed pins at 1 m intervals to estimate percent cover (%) of *grass*, *forb*, *shrub*, *litter*, *coarse woody debris*, *bare soil*, and *rock*. Percent cover was calculated as the proportion of pins intercepting each category. We also counted the number of dung piles in each transect to calculate *dung density* (dung ha^{-1}). Finally, we collected 4 soil cores (0 – 10 cm), homogenized them, and later determined *total nitrogen* (%) and *carbon to nitrogen ratio* at the Agricultural Analytical Services Laboratory at Penn State (University Park, PA).

Geospatial data

We used geospatial data to quantify landscape context at nested spatial extents around sampling plots in the study. To do so, we mapped live tree canopy cover using object-based image analyses on the NAIP imagery. 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. Although we produced robust "tree" and "no tree" classes, we could not assess the age structure of the "tree" class. As a result, we assumed trees were mature and seed-producing, which was a major assumption in the study.

Following map creation, we quantified landscape context using the landscapemetrics package (Hesselbarth et al. 2019) in R version 3.6.1. Specifically, we quantified: *percentage of landscape* (percentage of landscape with seed source; 0 to 100%), mean *fractal dimension* (seed source arrangement less or more complex; 1.0 to 2.0), and *contagion* (more complex with classes dispersed/interspersed equally or less complex with one class dominating the landscape exclusively; 0 to 100) (**Figure 3**). 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 (**Figure 4**).

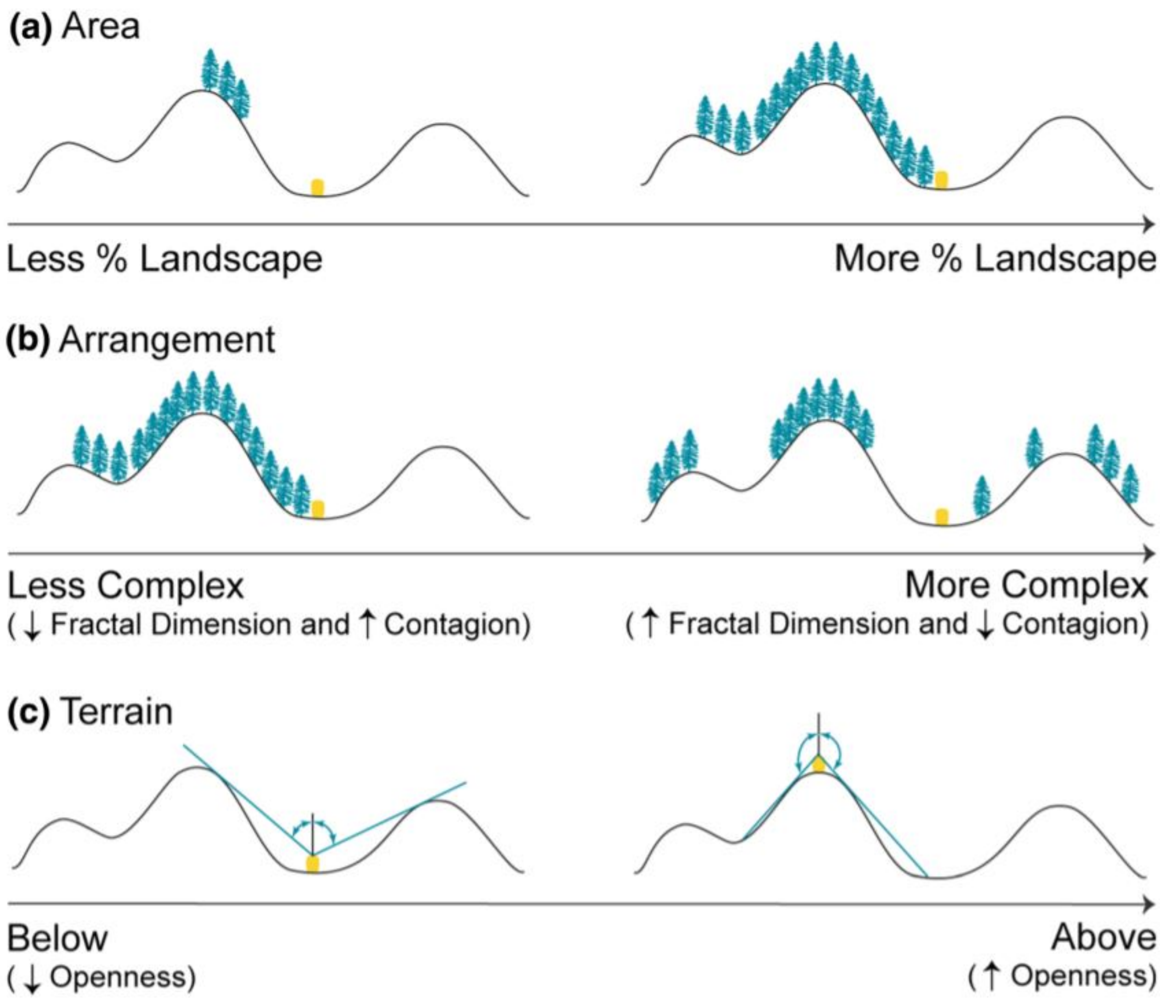

Figure 3. We used three metrics to measure seed source area and arrangement in the study. Seed source area (**a**) was measured using percentage of landscape and arrangement (**b**) was measured using mean fractal dimension and contagion collectively. We measured both area and arrangement because two 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.

We also used geospatial data to quantify terrain – allowing us to incorporate how surrounding topography affects seed delivery. For each 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°). 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. We did not use a 25 m radius because the toolbox calculates openness at 10 m intervals only.

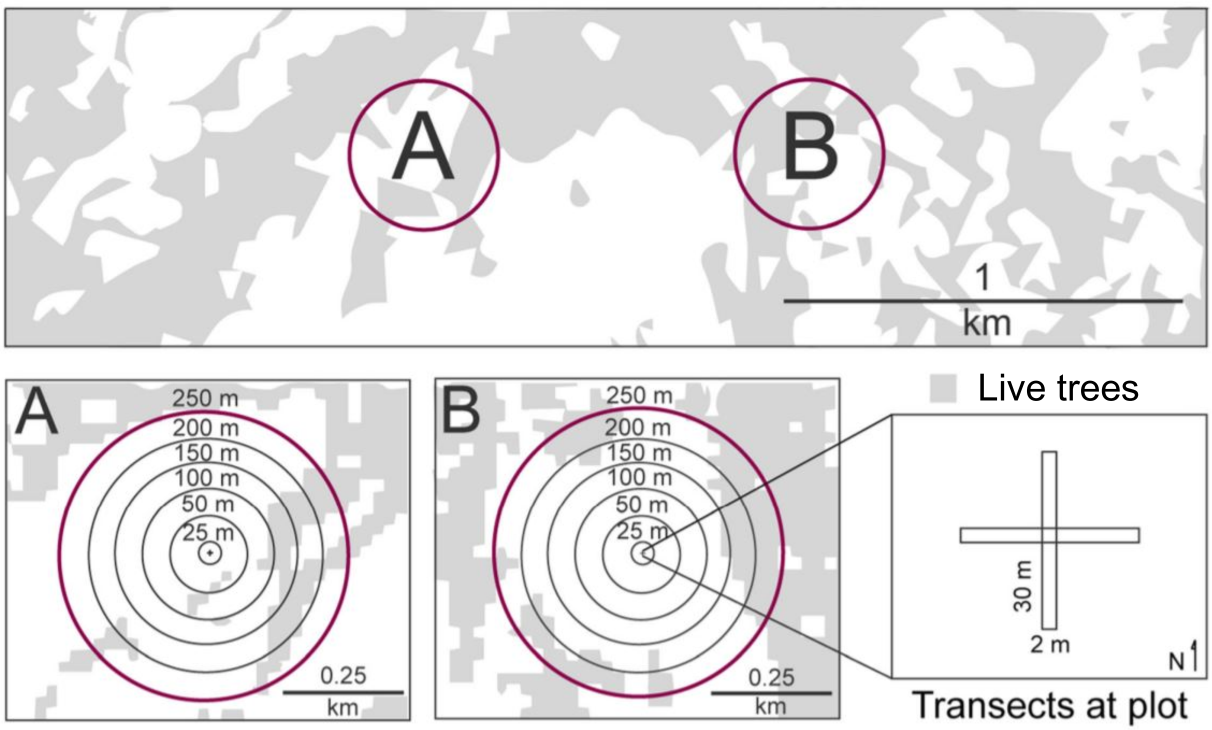

Figure 4. We measured seed source area and arrangement around plots at nested spatial extents: 25 m, 50 m, 100 m, 150 m, 200 m, and 250 m radii. In the field, we used transects at each plot to calculate tree species presence, regeneration density, and stocking density. We then related seed source area and arrangement to the field data, allowing us to test the effect of landscape context at different spatial extents on post-fire tree recovery.

Finally, we used geospatial data to estimate local water availability. Specifically, we created geospatial data layers (30 m resolution) on annual *climatic water deficit* (mm) and *actual evapotranspiration* (mm) using the Climatic Water Deficit Toolbox in ArcMap 10.6.1 (Dilts 2014). The toolbox estimated both variables with a modified Thornthwaite water balance model (Lutz et al. 2010) and monthly PRISM climate data (4 km resolution) on precipitation, maximum temperature, and minimum temperature. The climate data was downscaled using available water capacity (0 – 150 cm) for soils from STATSGO2 (30 m resolution) and a digital elevation model (1/3 arc-second resolution) from the USGS 3D Elevation Program. Following map creation, we calculated cumulative climatic water deficit and actual evapotranspiration at each plot center during the 4 years after the Boulder and Bull Fire, respectively. Doing so allowed us to capture local water availability during the time that most post-fire establishment occurs in the Northern Rockies (Harvey et al. 2016).

Data analysis

We created a series of generalized linear models to identify the spatial extents that tree species respond to landscape context. We used logistic regression to model the probability of tree species presence during post-fire tree recovery. Additionally, we used negative binomial regression to model regeneration density. For both modeling efforts, we used the full dataset (n = 71) 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-dispersed seeds, we assigned these tree species to their predominant regeneration trait. To underscore the spatial extents in which tree species responded to landscape context, we assessed whether seed source area and arrangement were a significant coefficient ($p < 0.05$) at each spatial extent. For models with significant coefficients, we plotted them against predicted values to better visualize relationships between seed source area and arrangement and regeneration density.

We used Random Forests (Breiman 2001) to investigate how local and landscape variables affect post-fire tree recovery. Like the generalized linear models, we used the full dataset (n = 71) to predict tree species presence and built species-level models that captured different regeneration traits: subalpine fir for wind-dispersed, lodgepole pine for serotiny, and quaking aspen for resprouting. Additionally, to predict stocking density, we used a data subset that included plots where conifer regeneration was observed (n = 44). We then built a model that classified whether a plot was stocked (>400 conifer stems acre^{-1}) or unstocked (<400 conifer stems acre^{-1}) (United States Forest Service 2015). Afterward we determined the relative impact of local and landscape variables by calculating their mean decrease in accuracy. If landscape variables were more influential than local variables, then we expected landscape variables to have a larger mean decrease in accuracy. Finally, to visualize potential thresholds, we generated partial dependence plots for predictor variables with >15% mean decrease in accuracy.

Results and Discussion

Post-fire tree regeneration

We observed post-fire tree regeneration in 60 of the 71 plots sampled. At the species level, subalpine fir, Engelmann spruce, and Douglas fir were present at 30, 8, and 12 plots respectively (**Figure 5**). Lodgepole pine was present at 28 plots and both serotinous and non-serotinous cones were observed on nearby surviving trees. Quaking aspen resprouts were present in 31 plots. Collectively, conifer regeneration occurred at 44 plots, but we observed wide variation in density. Mean densities for subalpine fir, Engelmann spruce, and Douglas fir were 247, 165, and 104 stems acre^{-1} respectively. Lodgepole pine was 685 stems acre^{-1}. After implementing the stocking threshold (>400 conifer stems acre^{-1}), 20 plots were considered stocked during the Random Forests analysis.

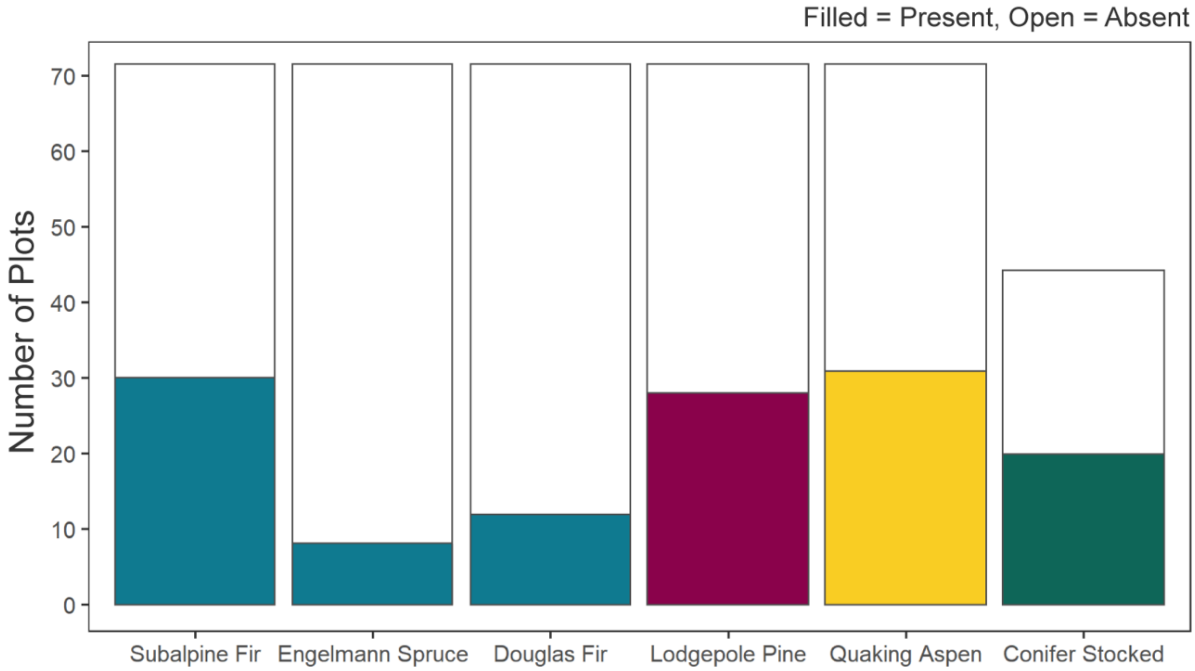

Figure 5. We sampled post-fire tree regeneration at 71 plots in the Boulder and Bull Fires. Graphs show the number of plots where tree species were present. Tree species are grouped by their predominant regeneration trait (blue = wind-dispersed, pink = serotiny, or yellow = resprouting). For the 44 plots with conifers were present, 20 were stocked (>400 conifer stems acre^{-1}).

Key spatial extents

Our findings provided insights into the influence of landscape context on post-fire tree recovery. Interestingly, we found that straight-line distance to nearest seed source sufficiently estimated tree species presence, but seed source area and arrangement were 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. 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 were 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 ponderosa 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 increased with increasing seed source area (**Figure 6**), reinforcing that the total seed source (not just the nearest seed source) shapes regeneration density. Additionally, terrain mattered at 100 m, such that complex seed source arrangements above burned areas at this scale supported the highest subalpine fir regeneration density (**Figure 7**).

For lodgepole pine and quaking aspen, seed source area and arrangement were relevant at 25 m, underscoring the ways fire triggers on-site seeds and propagules to facilitate recovery. At 25 m, lodgepole pine regeneration increased with decreasing seed source area and arrangement complexity. Most likely the absence of seed source is a signal of burn severity. High severity fires reduce live tree canopy cover (our proxy for seed source), but trigger on-site serotinous

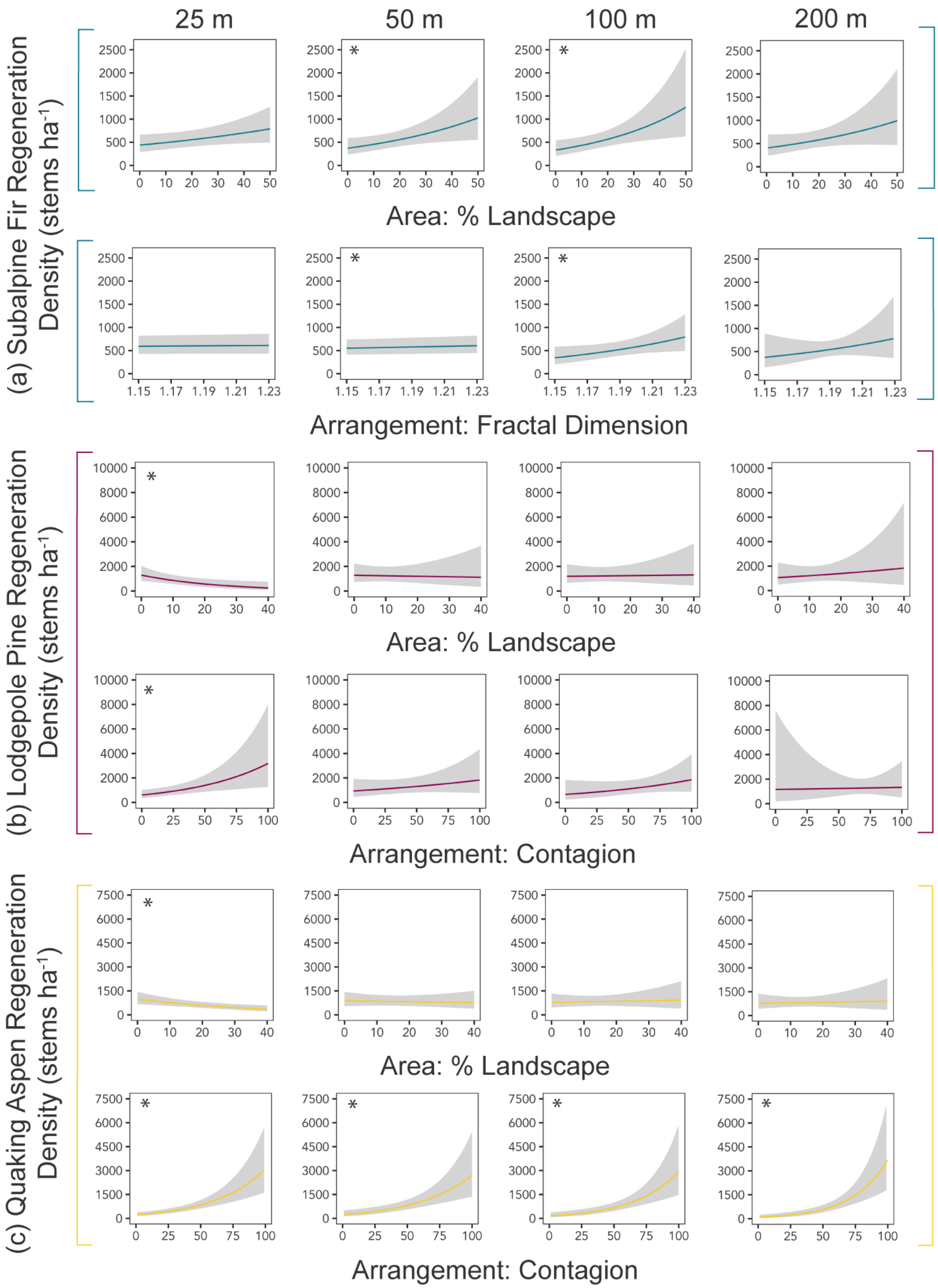

Figure 6. Seed source area and arrangement had scale-dependent effects on subalpine fir (**a**), lodgepole pine (**b**), and quaking aspen (**c**) recovery. Graphs show predicted regeneration densities (shaded areas reflect 95% confidence intervals) across levels of area and arrangement respectively. Brackets group together fixed effects used in the same model. Asterisks indicate a significant coefficient at that spatial extent ($p < 0.05$).

cones to open (Lotan 1976). As a result, lodgepole pine can recover prolifically after burning at high severity. Similarly, at 25 m, quaking aspen regeneration increased with decreasing seed source area and arrangement complexity. Given that quaking aspen resprouts from on-site root structures following high severity fire, the absence of seed source might again be a signal of 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.

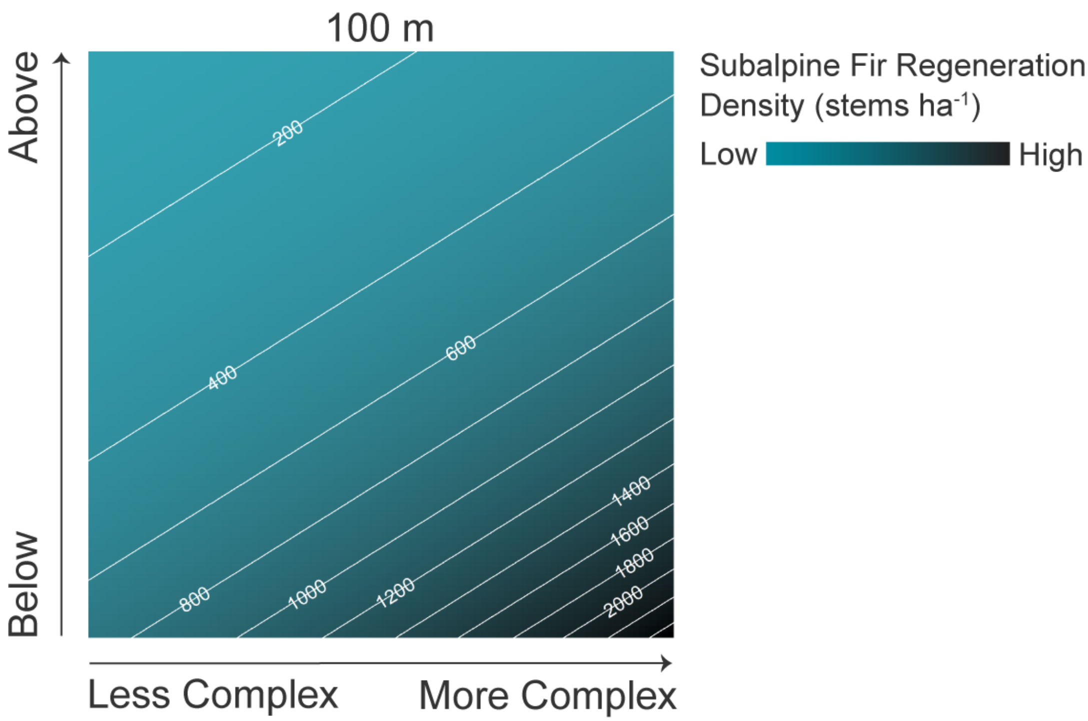

Figure 7. For subalpine fir, terrain mediated relationships between seed source arrangement and regeneration density. Specifically, we observed terrain-dependent effects at 100 m spatial extents, where plots positioned below more complex arrangements supported the highest subalpine fir regeneration density.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

Relative influence of landscape context and local site conditions

We found that landscape context – specifically seed source areas at 100 m and seed source arrangement at 25 m – was an important factor in subalpine fir presence and stocking density (**Figure 8**). But as expected, thresholds for achieving subalpine fir presence and stocking density differed. For subalpine fir presence, 10% of the surrounding 100 m needed to contain seed sources. Conversely, a higher threshold of 40% was required to reach *stocking density* (>400 stems acre^{-1}; United States Forest Service 2015). Different thresholds likely reflect that achieving tree species presence requires fewer seeds from surviving trees than reaching stocking density. Additionally, at 25 m, homogenous landscapes were most likely to support stocking density. The finding likely reflects how homogenous, high severity fires trigger opening of serotinous cones in lodgepole pine canopies (Lotan 1976). **Collectively, due to these diverse processes at play, it is critical to define explicitly whether maintaining forest composition (captured with tree**

species presence) or forest structure (captured with stocking density) is the goal when anticipating resilience to fire (Carpenter et al. 2011).

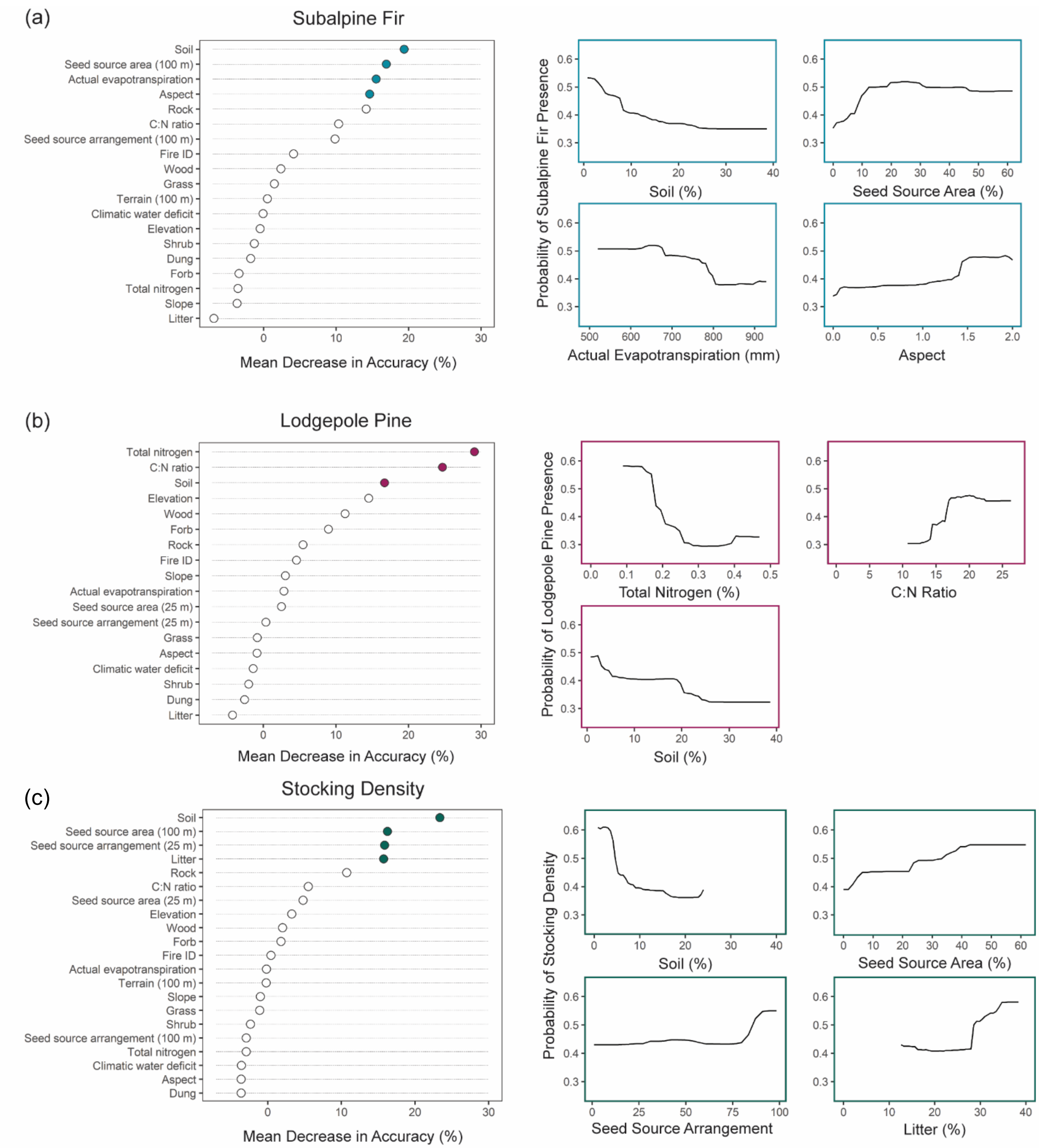

Figure 8. Random Forests revealed which local and landscape variables were important for subalpine fir (**a**) and lodgepole pine (**b**) being present at 71 plots. It also showcased which factors were important for 44 plots with conifer regeneration being stocked (>400 conifer stems acre^{-1}) (**c**). Variable importance was ranked using mean decrease in accuracy. Additionally, to evaluate the relationships between important variables and species presence, partial dependence plots were graphed for variables with a mean decrease in accuracy >15%.

Although landscape context was associated with subalpine fir presence and stocking density, it was not associated with lodgepole pine presence. Instead, local factors – specifically soil nutrients and soil cover – were most important. Associations with soil nutrients likely reflects ecosystem-level dynamics in which lodgepole pine is preferentially present on low-nutrient sites (Smithwick et al. 2005) because of its ability to persist in nutrient-poor environments. Recently, Turner et al. (2019) showed that 80% of total nitrogen recovery was achieved in 25 years after fire in lodgepole pine stands in Yellowstone National Park. Interestingly, the N accretion in biomass could not be accounted for by soil N pools or other N sources such as atmospheric deposition, suggesting a role for symbiotic N fixation in association with lodgepole pine roots (Turner et al. 2019). Additionally, lodgepole pine presence decreased with increasing soil cover, reinforcing the importance of local conditions for tree establishment.

Science delivery activities

Our study resulted in three core deliverables: two publications in peer-reviewed journals and an ArcGIS StoryMap. To make managers aware of these core deliverables, we wrote a research brief for the Northern Rockies Joint Fire Science Exchange Network. It will be circulated in October 2021. Additionally, the study contributed to Peeler's dissertation and presentations at the Ecological Society of America and American Geophysical Union Annual Meetings. A more detailed description of these science delivery activities can be found in Appendix B.

Conclusions and Implications for Management and Future Research

Our study unraveled spatial dynamics to better account for the role of landscape context in post-fire tree recovery. To do so, we reduced knowledge gaps on interactions among seed area and arrangement, tree regeneration traits, scale, terrain, and local site conditions across heterogenous post-fire environments. In reducing these knowledge gaps, findings moved us closer to creating resilient forest landscapes – a goal at the forefront of co-existing with fire in a warmer, drier world. 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 (National Forest Management Act 1976). To meet these two goals, placing a burned site in their landscape context could be fundamental to anticipating their resiliency and whether it restocks naturally. Accordingly, our findings provide considerations and thresholds to guide manager decision-making.

Resiliency describes the capacity of a system to "spring back" after a disturbance event to its original composition, structure, or function (Walker et al. 2004). Resiliency is challenging to quantify but defining the resilience of *what* to *what* and accounting for scale are good starting points (Carpenter et. al 2011). If anticipating resilience of *forest composition* to *fire* at the stand-level over successional cycles, then 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 their associations with regeneration density. However, seed source area and arrangement must be measured at relevant spatial extents that reflect predominant regeneration traits.

When accounting for landscape context, managers must account for the predominant regeneration trait. For example, subalpine fir is predominately wind-dispersed and relies on nearby surviving propagules to regenerate after fire. As a result, influential spatial extents for subalpine fir includes 50 m or 100 m – aligning with findings in other predominately wind-dispersed forests (Haire and McGarigal 2010; Coop et al. 2019; Downing et al. 2019) and known seed dispersal distances (McCaughey et al. 1986). Additionally, subalpine fir presence requires 10% seed source area at 100 m spatial extents, while stocking density (defined here as >400 conifer stems acre^{-1}; United States Forest Service 2015) requires 40%. Below these thresholds, burned sites are unlikely to restock naturally. However, for subalpine fir, managers must also consider terrain. Even though a burned site might be surrounded with sufficient seed source, its position in the landscape can impede recovery. For instance, burned sites positioned above surrounding seed source are most at risk of not restocking naturally.

Although landscape context is important for predominantly wind-dispersed tree species, it is less critical for ones that regenerate from seed sources and propagules found locally. For example, 25 m is a relevant spatial scale for lodgepole pine and quaking aspen – underscoring how fire triggers local seeds and propagules for recovery. For both tree species, regeneration increases with decreasing seed source area and arrangement complexity. Most likely the absence of seed source is a signal for burn severity. Furthermore, measuring local factors – specifically soil nutrients and soil cover – is important for anticipating lodgepole pine recovery. Associations with soil nutrients likely reflects ecosystem-level dynamics in which lodgepole pine is preferentially present on low-nutrient sites because of its ability to persist in nutrient-poor environments. Collectively, accounting for spatial dynamics among seed source area and arrangement, tree regeneration traits, scale, terrain, and local site conditions could help managers better anticipate resiliency and which burned sites will not restock naturally.

Implications for future research

We suggest two future directions for studying and managing tree regeneration across heterogeneous post-fire environments. First, future work that addresses similar objectives beyond our geographic scope would confirm whether landscapes trends hold across different forest types. For example, warmer, drier post-fire climates are occurring more frequently and are especially challenging to low-elevation montane forests (Stevens-Rumann et al. 2018; Davis et al. 2019; Rodman et al. 2020). In these forest types, water availability may be a limiting factor that overwhelms the relative influence of landscape context after fire. To test landscape trends across forest types, a starting point might be using datasets in western United States forests that measured seed sources using similar workflows with NAIP imagery (Coop et al. 2019; Downing et al. 2019; Walker et al. 2019). Secondly, terrain affects post-fire tree regeneration through interactive processes that include creating favorable local microclimates for establishment (Dobrowski 2011) and influencing landscape-level 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 landscape and local factors on post-fire tree recovery.

Literature Cited

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA (1987) Ecological neighborhoods scaling environmental patterns. Oikos 49:340-346

Beers TW, Peter ED, Wensel LC (1966) Notes and observations: aspect transformation in site productivity research, J For 64: 691-692

Breiman, L (2001). Random forests. Machine Learning 45: 5-32

Carpenter S, Walker B, Anderies JM, Abel N (2011) From metaphor to measurement: resilience of what to what? Ecosystems 4:765-781

Coop JD, DeLory TJ, Downing WM, Haire SL, Krawchuk MA, Miller C, Parisien MA, Walker RB (2019) Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes. Ecosphere 10:e02809

Davis KT, Dobrowski SZ, Higuera PE, Holdon ZA, Veblen TT, Rother MT, Parks S, Sala A, Maneta MP (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci U S A 116: 6193-6198

Dilts, TE (2014) Climatic Water Deficit Toolbox for ArcGIS 10.1. University of Nevada Reno

Dobrowski SZ (2011) A climate basis for microrefugia: the influence of terrain on climate. Glo Change Bio 17: 1022-1035

Donato DC, Harvey BJ, Turner MG (2016) Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? Ecosphere 7:e01410

Downing WM, Krawchuk MA, Meigs GW, Haire SL, Coop JD, Walker RB, Whitman E, Chong G, Miller C (2019) Influence of fire refugia spatial pattern on post-fire forest recovery in Oregon's Blue Mountains. Landsc Ecol 34:771-792

Haire SL, McGarigal K (2010) Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (Pinus ponderosa) in New Mexico and Arizona, USA. Landsc Ecol 25:1055-1069

Hart SC, DeLuca TH, Newman GS, et al (2005) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. For Ecol Manage 220:166–184

Harvey BJ, Donato DC, Turner MG (2016) High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655-669

Hesselbarth MHK, Sciaini M, With KA, Wiegand K, Nowosad J (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42: 1648-1657 (ver. 1.4)

Katul GG and Poggi D (2012). The effects of gentle topographic variation on dispersal kernels of inertial particles. Geophys Res Lett 39: L03401

Kemp KB, Higuera PE, Morgan P (2016) Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landsc Ecol 31:619-636

Lotan J (1976) Cone serotiny – fire relationships in lodgepole pine. Proc Tall Timbers Fire Ecol Conf 14: 267-278

Lutz JA, van Wagtendonk JW, Franklin JF (2010) Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. J Biogeogr 37: 936-950

Lyon LJ, Stickney PF (1974) Early vegetal succession following large northern Rocky Mountain fires. Proc Tall Timbers Fire Ecol Conf 14: 355-375

Metzger KL, Smithwick EAH, Tinker DB, Romme WH, Balser TC, Turner MG (2008) Influence of coarse wood and pine saplings on nitrogen mineralization and microbial communities in young post-fire *Pinus contorta*. For Ecol Manag 265-67

McCaughey WW, Schmidt W, Shearer RC (1986) Seed dispersal characteristics of conifers in the inland mountain west. In: Proceedings – Conifer Tree Seed in the Inland Mountain West Symposium. United States Forest Service, Department of Agriculture, General Technical Report INT-203, pp50-62
National Forest Management Act (1976) https://www.fs.fed.us/emc/nfma/includes/NFMA1976.pdf Accessed 1 March 2021
O'Neill, RV (1989) Transmutations across hierarchical levels. In: Innis GS and O'Neill RV (eds) Systems Analysis of Ecosystems. International Cooperative Publishing House, Maryland, pp 59-78
Reader RJ and Buck J (1986) Topographic variation in the abundance of *Hieracium floribundum*: relative importance of differential seed dispersal, seedling establishment, plant survival and reproduction. J Ecol 74: 815-822
Rodman KC, Veblen TT, Battaglia MA, Chambers ME, Fornwalt PJ, Holden ZA, Kolb TE, Ouzts JR, Rother MT (2020) A changing climate is snuffing out post-fire recovery in montane forests. Glob Ecol Biogeogr 29: 2039-2051
Rother MT, Veblen TT (2016) Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7:e01594
Rowe JS (1983) Concepts of fire effects on plant individuals and species. In: Wein RW and MacLean DA (eds) The Role of Fire in North Circumpolar Ecosystems. John Wiley & Sons Ltd, New Jersey, pp 135-154
Schoennagel T, Turner MG, Romme WH (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84:2967-2978
Smithwick EAH, Turner MG, Mack MC, Chapin FS (2005) Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems 8:163-181
Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2018) Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21: 243-252
Trakhtenbrot A, Katul GG, Nathan R (2014) Mechanistic modeling of seed dispersal by wind over hilly terrain. Ecol Model 274: 29-40
Turner MG (2005) Landscape Ecology: What Is the State of the Science? Annu Rev Ecol Evol Syst 36:319-344
Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol Monogr 67:411-433
Turner MG, Romme WH, Reed RA, Tuskan GA (2003) Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape. Landsc Ecol 18:127-140
Turner MG, Whitby TG, Romme WH (2019) Feast not famine: Nitrogen pools recover rapidly in 25-yr-old postfire lodgepole pine. Ecology 100: e02626
United States Forest Service (2015) Bridger-Teton National Forest: Land and Resource Management Plan. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3840286.pdf. Accessed 24 February 2021
Walker RB, Coop JD, Downing WM, Krawchuk MA, Malone SL, Meigs GW (2019) How much forest persists through fire? High-resolution mapping of tree cover to characterize the abundance and spatial pattern of fire refugia across mosaics of burn severity. Forests 10:782
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385-397

Wildland Fire Leadership Council (2014) A National Cohesive Wildland Fire Management Strategy. https://www.forestsandrangelands.gov/documents/strategy/strategy/CSPhaseIII NationalStrategyApr2014.pdf. Accessed 24 January 2020

Zakšek K, Oštir K, Kokalj Ž (2011) Sky-view factor as a relief visualization technique. Remote Sens 3:398-415

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Appendix B: List of Scientific Publications and Science Delivery Products

Table B1. The JFSP GRIN Award facilitated two scientific publications and five science delivery products.

Deliverable	Title	Status
Article in Peer-Reviewed Journal	Peeler JL and Smithwick EAH. 2020. Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery. *Landscape Ecology*, 35, 9, 1945-1959	Published
Article in Peer-Reviewed Journal	Peeler JL and Smithwick EAH. 2021. Interactions between landscape and local factors inform spatial action planning in post-fire forest environments. *Landscape Ecology*	Published
ArcGIS StoryMap	Peeler JL. The shape of landscapes. 2021. https://arcg.is/Damzj	Published
JFSP Northern Rockies Research Brief	Effects of seed source pattern on post-fire tree recovery	Under Review (Anticipated Publication in October 2021)
JFSP Final Report	Scale-dependent effects of landscape context on post-fire forest regeneration in the Northern Rockies	Under Review
Dissertation	Peeler JL. 2021. The role of landscape context in forests recovering from fire. The Pennsylvania State University	Published
Scientific Poster	Peeler JL and Smithwick EAH. 2019. Scale-dependent effects of landscape context on post-fire forest regeneration in the Northern Rockies. American Geophysical Union. San Francisco, CA	Completed

Scientific Poster	Peeler JL and Smithwick EAH. 2020. Live seed source and terrain have scale-dependent effects on post-fire tree recovery. Ecological Society of America. Virtual due to COVID-19	Completed

Appendix C: Metadata

Following the data management plan, our data was archived through Penn State's DataCommons service (Metadata DOI: http://doi.org/10.26208/96gx-qb80) and shared with the Forest Service R&D data archive to provide access to the scientific and management community. Archival with the Forest Service R&D data archive is currently under way. At both archives, we provide access to field data collected at 71 plots in the Boulder and Bull Fires near Jackson, Wyoming, United States. The field data includes information on species-level tree regeneration, terrain, ground cover, and soil nutrients. Additionally, we provide access to the R script, field plot location shapefiles, and post-fire tree cover rasters used to calculate seed source pattern at nested spatial scales (25 m, 50 m, 100 m, 150 m, 200 m, 250 m radii).