

Where do they come from; Where do they grow? Postfire conifer seed dispersal and establishment in rugged terrain

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ABSTRACT

Changing fire regimes and climate can disrupt postfire tree regeneration in obligate seeders by increasing distances to seed sources and creating unsuitable establishment conditions. Complex topography could buffer these effects by enhancing seed dispersal or providing microclimates suitable for seedling establishment. In two field experiments on the Bridger-Teton National Forest (Wyoming, USA), we assessed effects of complex topography on: (1) conifer seed dispersal, (2) lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) germination and seedling establishment, and (3) microclimate. We trapped seeds in areas of stand-replacing fire along a ruggedness gradient and planted seeds in burned areas that varied in ruggedness (rugged or gentle) and terrain shape (concave or convex). Rugged terrain enhanced lodgepole pine seed delivery frequency, and seed delivery 60 m from a seed source was almost two times greater in rugged (~9% of total seed pressure) vs. gentle terrain (~5%). Seed delivery did not vary upslope vs. downslope of mature forest. The proportion of seeds that germinated was lower in rugged vs. gentle terrain (lodgepole pine: 0.07 vs. 0.19, Douglas-fir: 0.03 vs. 0.10), and germination of lodgepole pine was enhanced in concave terrain. Rugged sites lost soil moisture rapidly and were drier than gentle sites across the growing season, and concave, rugged sites were warmer than gentle sites or convex rugged sites. The counteracting effects of terrain ruggedness on seed dispersal and seedling establishment could produce complex spatial patterns of tree regeneration that are not readily explained by distance to seed source.

1. Introduction

Changing fire regimes can alter forest composition and structure (Prichard et al., 2017) with the potential for post-disturbance loss of resilience when regeneration mechanisms are disrupted (Turner et al., 2019; Coop et al., 2020; Rammer et al., 2021; Seidl and Turner, 2022). Species and population traits are adapted to historical disturbance regimes (Muir and Lotan, 1985; Pausas and Keeley, 2014; Johnstone et al., 2016), but climate change is pushing fire regimes outside their historical ranges of variability and threatening forest recovery (Cansler and McKenzie, 2014; Abatzoglou and Williams, 2016; Higuera et al., 2021; Parks et al., 2025). Postfire regeneration of non-resprouting trees that lack an *in-situ* seedbank (e.g., Douglas-fir, *Pseudotsuga menziesii*; Engelmann spruce, *Picea engelmannii*; and non-serotinous lodgepole pine, *Pinus contorta* var. *latifolia* in the western US) depends on seed dispersal into burned areas (Greene and Johnson, 2000) and local conditions conducive to seed germination and establishment (Davis et al., 2018). Short fire-return intervals (Keeley et al., 1999; Brown and

Johnstone, 2012; Gill et al., 2021; McColl-Gausden et al., 2022) and larger patches of high-severity fire (Gill et al., 2022) may result in insufficient seed supply to restock burned areas. Unfavorable temperature and moisture conditions can further compromise postfire forest recovery (Harvey et al., 2016; Stevens-Rumann et al., 2018; Hansen and Turner, 2019; Rodman et al., 2020; Hoecker et al., 2020; Davis et al., 2023), and these effects are stronger on seedlings than mature trees (Anderson-Teixeira et al., 2013; Dobrowski et al., 2015). Thus, as changing fire regimes and climate threaten forest recovery, it is critical to understand mechanisms that may influence both seed delivery and seedling establishment (McDowell et al., 2020).

Although suitable climate for subalpine conifers is expected to decline as temperatures warm (Hansen and Phillips, 2015; Hansen et al., 2018), simulation models suggest that complex topography may delay state-changes from forest to non-forest ecosystems (Albrich et al., 2020; Turner et al., 2022). Rugged terrain is characterized by differences over short distances in slope, elevation, and aspect, all of which affect regeneration (Hoecker et al., 2020; Kiel and Turner, 2022; Willson and

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Hurteau, 2024; Kuo et al., 2026). Microclimate in topographically complex regions can also differ substantially from the broader climate (Daly et al., 2010; Dobrowski, 2011), which may retain some areas with temperature and moisture conditions suitable for species to establish despite a warming, drying climate. Further, dynamic wind patterns in rugged topography may enhance dispersal by encouraging uplifting that allows seeds to travel farther (Nathan et al., 2002; Trakhtenbrot et al., 2013). Thus, rugged terrain may enhance conifer regeneration by increasing seed delivery and buffering microclimate if physical conditions (e.g., slope) are not too harsh.

In the Greater Yellowstone Ecosystem (GYE; Wyoming, USA), rugged terrain may shape postfire forest recovery (Turner et al., 2022; Keller and Turner *In press*). However, future postfire regeneration is uncertain for two dominant conifers (lodgepole pine and Douglas-fir), and effects of rugged terrain on seed dispersal and seedling establishment could influence their future distributions (e.g., Conlisk et al., 2018; Turner et al., 2022; Knowlton et al., 2025). Lodgepole pine occupies much of the subalpine zone, and serotinous populations regenerate robustly within burned areas as heat releases seeds from canopy seed banks (Schoennagel et al., 2006). However, non-serotinous populations depend on dispersal from live, mature seed sources. Douglas-fir is prevalent in the lower montane, and postfire regeneration also depends on seed dispersal from live, mature seed sources (e.g., Harvey et al., 2013, 2016). Postfire regeneration of each species has been well studied in the western US (e.g., Donato et al., 2009; Kemp et al., 2016; Harvey et al., 2016; Stevens-Rumann et al., 2018; Boag et al., 2020), but most field data in the GYE were collected on the more gentle topography of the central plateau (e.g., Turner et al., 1997, 1999, 2004). Field

experiments in gentle terrain have evaluated germination and establishment (e.g., Kueppers et al., 2017; Conlisk et al., 2018; Hansen and Turner, 2019; Hoecker et al., 2020) and seed dispersal (Gill et al., 2021), but whether complex topography may mediate observed patterns is unclear.

Here, we conducted complementary experiments in a rugged portion of the southern GYE to determine the effect of complex terrain on mechanisms underpinning postfire regeneration of lodgepole pine and Douglas-fir. We asked (1) How do the delivery and diversity of wind-dispersed conifer seeds into areas of stand-replacing fire vary with topography? (2) How do germination, establishment, and growth of lodgepole pine and Douglas-fir in recently burned patches vary with terrain ruggedness and shape? (3) How does soil microclimate vary with terrain ruggedness and shape? We expected rugged topography to facilitate seed dispersal by increasing seed delivery and allowing seeds to travel farther downslope of live forests. While we expected germination to be unaffected by terrain ruggedness and shape due to snow-melt saturating spring soils, we expected concave topography to increase seedling establishment by encouraging moisture retention in dry conditions. We anticipated soil microclimates would vary with ruggedness and terrain shape, with concave and gentle sites hosting greater soil moisture and concave rugged sites exhibiting lower temperatures resulting from cold air pooling (Daly et al., 2010; Dobrowski, 2011).

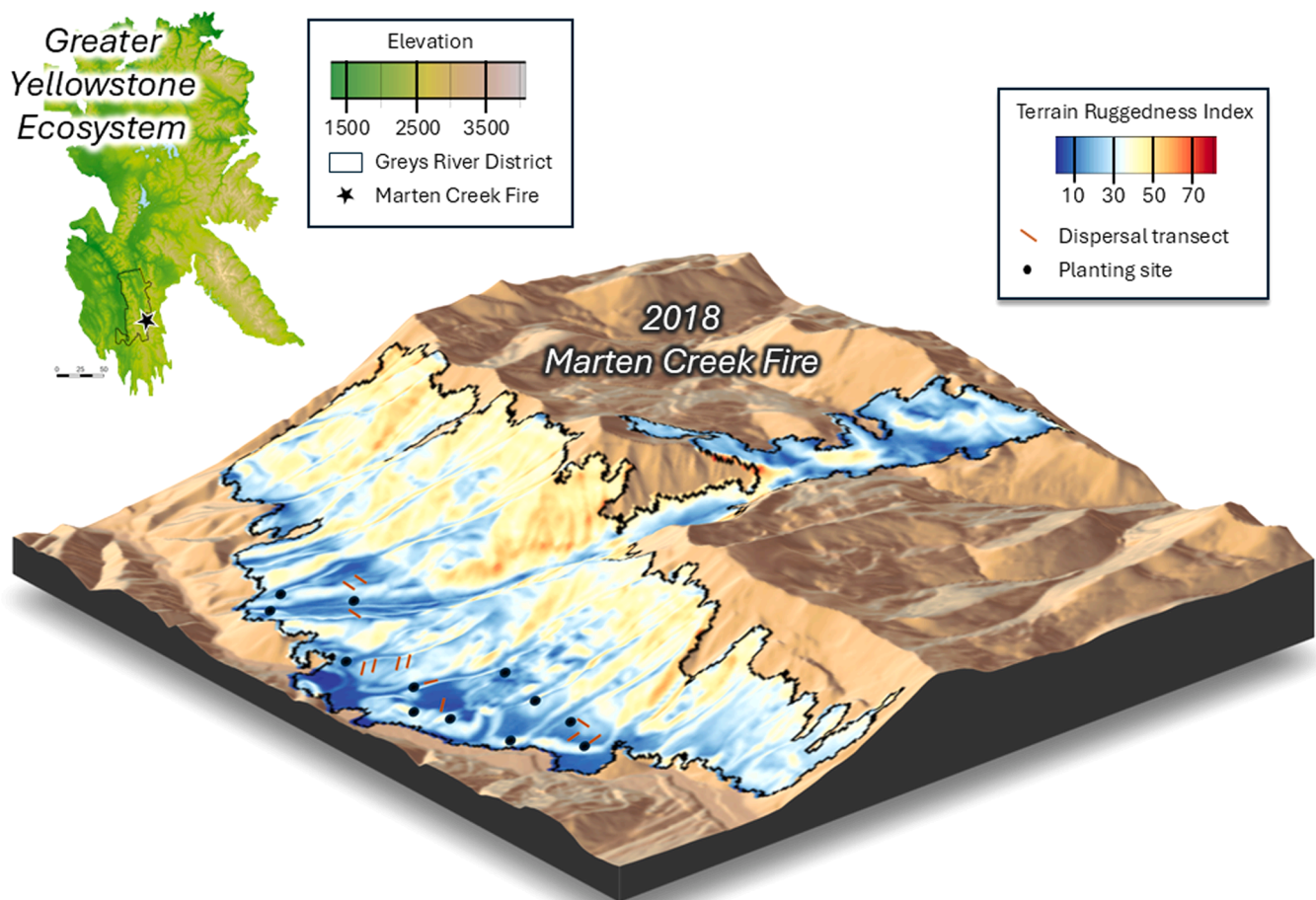


Fig. 1. Locations of dispersal transects and germination plots within the perimeter of the 2018 Marten Creek Fire on the rugged Greys River District of Bridger-Teton National Forest, Wyoming, USA. 3D terrain models were generated in R using the Rayshader package (Morgan-Wall, 2018).

2. Methods

2.1. Study area

All study sites were located within areas of high-severity fire in the 2018 Marten Creek Fire (2584 ha) on the Greys River District of Bridger-Teton National Forest (western Wyoming, USA, Fig. 1). Pre-fire forests were dominated by mature lodgepole pine. Mixed stands of mature Douglas-fir, lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) were also present on the landscape. Individual lodgepole pines can be serotinous and release seeds when heated or non-serotinous, releasing seeds annually as cones mature. Other conifers in the study area are non-serotinous. All dominant conifers release most seeds between August and October (McCaughy et al., 1985). The District is managed for multiple uses, including livestock grazing, recreation, and timber harvest. Clearcut timber harvests peaked in the 1960s, and lodgepole pine forests regenerated through both seedling plantings and natural regeneration (USFS, 2004).

Study site elevations ranged from 2200 m to 2450 m above sea level (asl) and were stratified across a gradient of terrain ruggedness (Fig. 1). Ruggedness was quantified by using the Terrain Ruggedness Index (TRI), calculated as the square root of the sum of squared differences in elevation between a focal cell and its eight neighboring cells (unitless, Riley et al., 1999). Median ruggedness within the Marten Creek Fire was 26 (Figure S1), and the ruggedness of our study sites ranged from 4.6 to 46.3 (calculated from a 30 × 30 m Digital Elevation Model, DEM). Geologic processes including thrust faulting, glaciation, stream erosion, and mass wasting formed this rugged landscape characterized by undulating mountain slopes, landscape benches, and landslides (USFS, 2004). Soils are primarily derived from sandstone, dolomite, and shale (USFS, 2004). The climate is continental, characterized by snowy winters and dry summers (Hostetler et al., 2021), but the Greys River District has notably wetter summers than elsewhere in the GYE (USFS, 2004). Precipitation during the growing season (June – August)

averages 16.26 cm, and average monthly temperature ranges from −6.7°C in December to 15.7°C in July (30-year climate normals, 1991–2020, Willow Creek observation station, NWCC, 2026). The historical fire regime in forests consisted of stand-replacing fires every 100–300 yr (Loope and Gruell, 1973; USFS, 2004; Jacobs and Whitlock, 2008).

2.2. Field methods

2.2.1. Q1 – Seed delivery and diversity

To estimate seed pressure within local mature forest, we established *seed-pressure transects* (50 m long, $n = 6$) consisting of seed collection trays in mature, live forest (Fig. 2). Four transects were placed in forests that had no evidence of previous logging, and to represent the variability in stand structure on the landscape, two transects were established in planted and previously logged, even-aged, mature lodgepole pines (hereafter, “planted stand”). Stand density was measured by tallying all cone-bearing trees by species within a 2 × 50 m belt transect. We recorded the height, diameter at breast height (DBH, 1.4 m), cone abundance category (<10, 10–50, 51–100, >100 cones tree^{−1}), and presence of serotinous cones (for lodgepole pine) for the closest cone-bearing tree every 2 m ($n = 25$) along each transect. Seed collection trays were placed every 2 m along each transect ($n = 24$ trays transect^{−1}). Trays measured 28 × 54 × 6 cm and were lined with landscape fabric to allow water drainage without seed loss. All seed trays were covered with 0.635 cm² mesh to prevent granivory while allowing seeds to fall through.

To quantify seed dispersal into burned forest, we established *dispersal transects* ($n = 12$) that extended 100 m into burned forest from a live-forest edge (Fig. 2). Dispersal transects were oriented either upslope ($n = 7$) or downslope ($n = 5$) of the live-forest edge along a gradient of terrain ruggedness (TRI ranged from 4.6 to 29.6). Transect TRI was calculated as the mean TRI of all 30 × 30 m cells crossed by the transect. Three transects originated from mature (>60 years old), cone-bearing

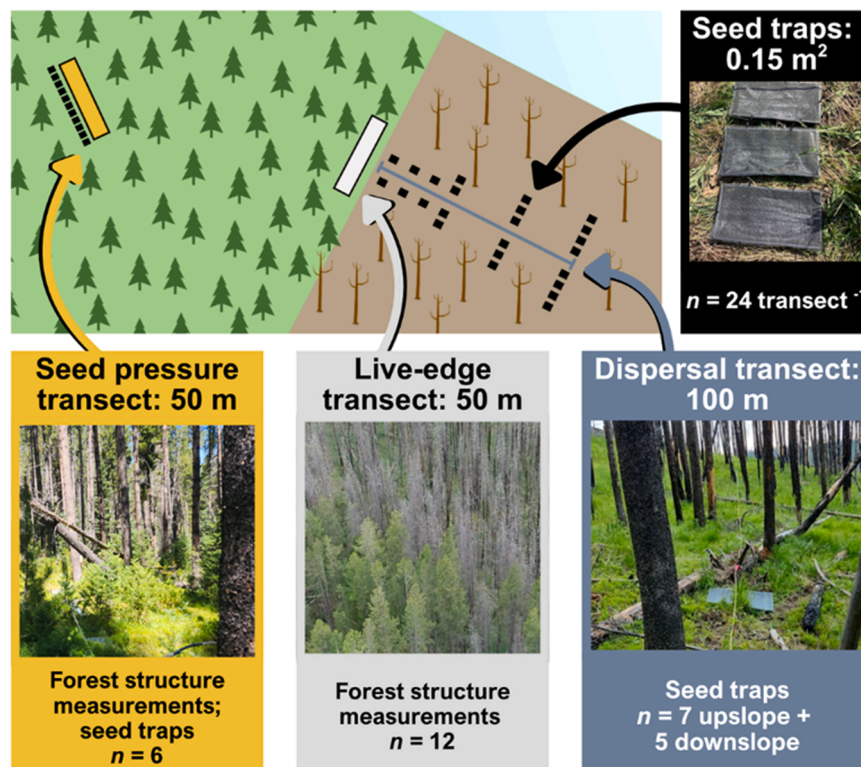


Fig. 2. Layout of the transects used to assess the density of seeds falling in mature, live forest (i.e. seed pressure), structure and composition of live-edge forests, and seed delivery into areas that burned at high severity (dispersal).

planted stands, and nine originated from mature naturally regenerated stands that had not burned in at least 100 years. Seed trays were placed at 5-, 20-, and 35-meters (two trays each); 50 m (four trays); 75 m (six trays); and 100 m (eight trays; total $n = 24$ trays transect⁻¹). Hereafter, the collection of trays at each distance is referred to as a seed trap ($n = 6$ seed traps transect⁻¹). Seed trap area increased with distance from the seed source because fewer seeds disperse at greater distances (Greene and Johnson, 1989; Nathan and Muller-Landau, 2000). Dispersal transects were separated by at least 100 m to minimize the potential for spatial autocorrelation. Seed traps were deployed from July to October of 2024 to align with local conifer seed set phenology (McCaughy et al., 1985). All traps were disassembled, and their contents bagged in early October, and conifer seeds were counted and identified to species in a laboratory.

To characterize local seed sources for each dispersal transect, we documented the structure, composition, and cone abundance of live, cone-bearing trees along 2×50 m *live-edge forest transects* ($n = 12$) parallel to burned edges and located 5 m within the live forest (Fig. 2). Live-edge forest transects were centered at and perpendicular to dispersal transects (Fig. 2). As for the seed-pressure transects, we recorded the height, DBH, cone abundance category (<10, 10–50, 51–100, >100 cones tree⁻¹), and presence of serotinous cones (for lodgepole pine) for the closest cone-bearing tree every 2 m along each live-edge transect ($n = 25$).

2.2.2. Q2 – Seedling establishment experiment

To address our second question, we planted seeds within a 2×2 factorial experiment varying local terrain shape (convex vs. concave) and terrain ruggedness (gentle vs. rugged) with three replicates of each combination ($n = 12$ plots, Fig. 3). Terrain shape was determined using the Topographic Position Index (TPI, De Reu et al., 2013), in which values less than zero signify concave terrain and values greater than zero

signify convex terrain, and ranged from -4.9 – 6.5 . Terrain ruggedness was determined using the TRI (Riley et al., 1999). Values of TRI ranged from 10.3 to 46.3, and we defined values ≤ 26 as gentle and > 26 as rugged, with 26 being the median TRI within the Marten Creek Fire (Fig. S1). Both TRI and TPI were calculated for a focal cell from the surrounding 8 cells with a 3×3 moving window from a 30×30 m DEM.

In each plot, we established planting arrays consisting of five groups of three planting trays ($28 \times 54 \times 6$ cm, $n = 15$ plot⁻¹) in summer 2024. One group was positioned at plot center with four groups positioned 7.5 m from center in each cardinal direction, as in Hoecker et al. (2020). Seeds were planted in October 2024 in trays with their bottoms removed so that seeds were in direct contact with mineral soil. Vegetation was cleared and the soil leveled in planting trays. Within each planting group, one tray was sown with 50 lodgepole pine seeds, one with 50 Douglas-fir seeds, and the third served as a control with no seed addition. Planting treatments were assigned at random for each of the five planting groups in a plot, and seeds were planted within an x-y grid within each tray. We used locally sourced seeds collected on the Greys River District from the USFS Lucky Peak Nursery in Boise, ID and conducted viability trials in the lab to determine germination baselines for both species.

Seed germination was recorded in the field in June 2025, and in late September 2025, we recorded mortality, defined as the proportion of germinants that died through the growing season (i.e., $mortality\ rate = \frac{dead\ germinants}{germinants}$), and establishment rates, defined as the proportion of sown seeds that survived the first growing season (i.e., $establishment\ rate = \frac{surviving\ seedlings}{sown\ seeds}$). To assess seedling growth, each surviving seedling was removed and photographed against a grid for estimating shoot and root lengths.

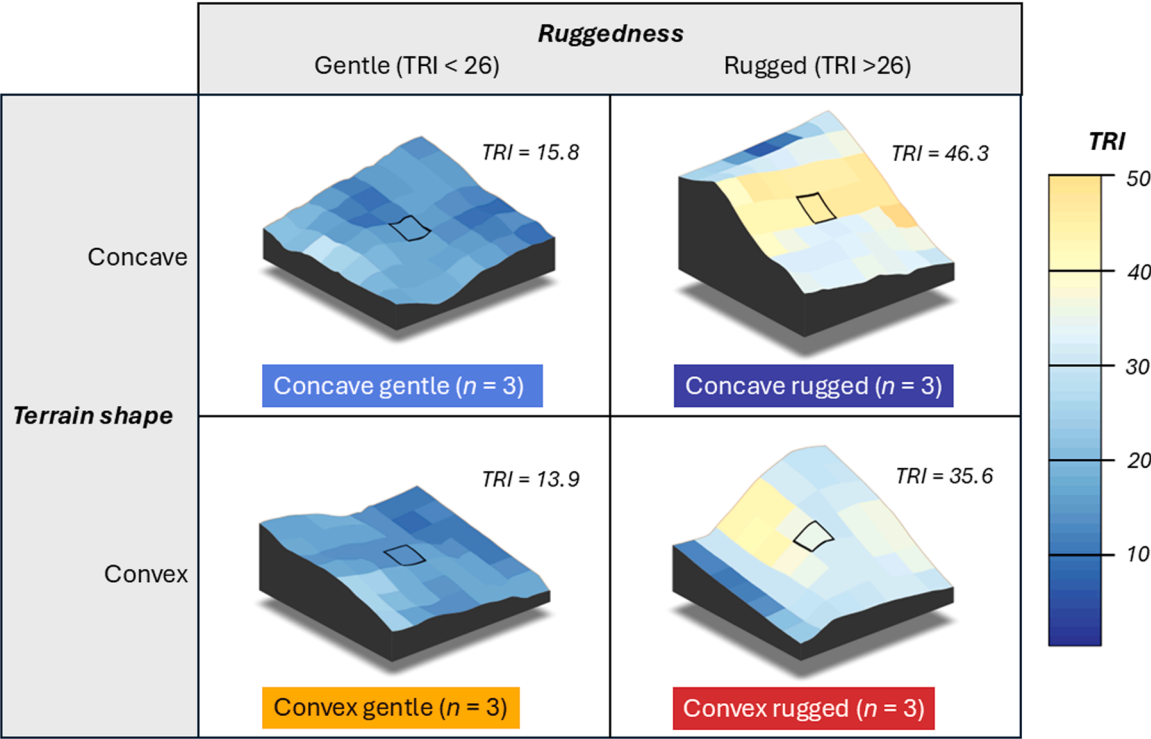


Fig. 3. Visualisations of four experimental planting sites to illustrate differences in terrain ruggedness (Terrain Ruggedness Index, TRI) and shape (Topographic Position Index, TPI). For illustrative purposes, three-dimensional terrain models were generated from a 1×1 m DEM, and the overlay shows the TRI values calculated from a 30×30 m DEM that was used in our analyses. The center cell, highlighted by a black square, represents the 30×30 m planting site. Planting sites followed a 2×2 factorial that varied terrain ruggedness (rugged and gentle) and shape (concave and convex). 3D models were generated in R using Rayshader package (Morgan-Wall, 2018).

2.2.3. Q3 – Soil microclimate variation and soil texture

Soil samples (15 cm depth) were collected in summer 2024 from the center of each planting plot, air dried in the field, and returned to the laboratory for texture analysis (percent sand, silt, and clay) using the hydrometer method (Bouyoucos, 1962). We instrumented each planting site with a Tomst TMS–4 datalogger (Wild et al., 2019) in June 2025 to track soil moisture and temperature (hereafter “soil microclimate”) at 15 min intervals through the growing season. Measurements of volumetric soil moisture were calibrated to the average sand, silt, and clay content across all plots. Dataloggers were placed in the control tray of the center group in each plot to track soil microclimate throughout the growing season. Temperature was measured 6 cm below the soil surface and moisture was measured for the top 12 cm of soil. Instrumentation was deployed through our final sampling in September 2025.

2.3. Data analysis

2.3.1. Question 1 – Seed delivery and diversity

All seed delivery results were standardized in units of seeds per square-meter, and analyses excluded any disturbed or damaged seed trays ($n = 5$ out of 144 seed-pressure trays and $n = 15$ out of 288 dispersal trays) to avoid underestimating delivery due to post-collection seed loss. To estimate maximum seed pressure excluding effects of terrain ruggedness and distance to seed source, we calculated species-specific and total seed pressure in live forest stands by summing the seeds collected in each tray by seed-pressure transect. We used Spearman’s correlations to relate basal area, cone abundance, and tree height with seed pressure in the live, mature forest. To detect an effect of forest characteristics on seed pressure despite our low sample size (i.e., to reduce Type II error), we set $\alpha = 0.10$ for these analyses. The maximum seed pressure observed in mature forests was used to estimate maximum potential seed pressure along the live-forest edge of each dispersal transect.

For each dispersal transect into burned areas, we summed seeds collectively and by species for each seed trap and for the entirety of each transect. Three transects trapped no seeds, so dispersal models were fit only for transects that successfully trapped seeds ($n = 9$). Because nearly all trapped seeds were lodgepole pine, transect total lodgepole pine seed delivery (log-transformed to meet model assumptions) was regressed against characteristics of live, cone-bearing lodgepole pines in the live-edge forest (height, cone abundance, basal area) using linear models (LMs). Models were compared using corrected AIC (AICc) for small sample sizes to determine which forest characteristics best explained total seed delivery into burned areas.

We fit two separate models to determine how terrain ruggedness affected lodgepole pine seed dispersal into burned areas (similar to Brown and Johnstone, 2012; Peeler and Smithwick, 2020). We estimated seed delivery frequency by distance (i.e., presence/absence of lodgepole pine seeds) by fitting a generalized linear model (GLM) with binomial errors. Candidate models included characteristics of the local terrain (ruggedness, upslope or downslope orientation relative to the live forest) and live-forest edge (basal area, height, cone abundance as potential proxies for seed pressure) added to and interacting with distance from the live-forest edge. Models were evaluated using AICc and Nagelkerke R^2 (Nagelkerke, 1991). Then, using only data from traps that collected seeds, we estimated a lodgepole pine seed dispersal density kernel by fitting linear models to seed delivery density by distance with terrain and forest characteristics as additional predictors. Seed delivery was log-transformed prior to analysis to meet normality assumptions (as in Greene and Johnson, 2000), and results are given as a proportion of maximum observed seed pressure in mature forest. The same model selection protocols were followed as for the seed delivery frequency model.

2.3.2. Question 2 – Seedling establishment

Seed germination, mortality, and establishment were measured at

the plot level ($n = 12$). Seeds sown in areas that had been damaged by animals at the time of assessment were excluded from the analysis. To determine species-level differences in germination and establishment (both logit-transformed to meet normality assumptions), we used two-sample t -tests, and we used a Kruskal-Wallis test to assess differences in mortality rates. We fit separate linear models for germination and establishment with terrain ruggedness (TRI value) and shape (TPI value) as predictors. Germination rates were logit transformed (as in Hoecker et al., 2020) prior to analysis to meet linear model normality and homoscedasticity assumptions. Seedling establishment models included log-transformed TRI values as a predictor variable when necessary to meet model assumptions. Models including terrain shape, ruggedness, and their additive and interactive effects were compared using AICc. To detect ecologically relevant differences in establishment rates despite our low sample size, we again set α at 0.10 for these analyses to minimize Type II error. Lastly, ANOVAs were used to determine if root-to-shoot length ratios differed by species, plot ruggedness, or terrain shape.

2.3.3. Question 3 – Soil microclimate variation

The TOMST dataloggers for volumetric soil moisture were calibrated to the average sand, silt, and clay content across all plots. Soil temperature and moisture were summarized daily at the plot level ($n = 12$) by terrain type ($n = 3$ replicates each) and were compared using Kruskal-Wallis tests. Sites with disturbed dataloggers ($n = 2$) were excluded from analysis beginning in the month when the disturbance occurred. LOESS curves were fit to the average daily soil temperature and moisture measurements to account for temporal correlations in weather across the growing season, and daily LOESS residuals (hereafter “detrended” data) were averaged by plot. Linear models were used to determine how terrain ruggedness and shape affected detrended soil temperature and moisture. Analyses for all questions were conducted in R (v4.4.1, R Core Team, 2024) with plotrix (Lemon, 2006), rcompanion (Mangiafico, 2026), terra (Hijmans et al., 2026), tidyverse (Wickham et al., 2019), rayshader (Morgan-Wall, 2018), and AICcmodavg (Mazerolle, 2023) packages.

3. Results

3.1. Q1 – Seed delivery and dispersal

Seed pressure in mature live forest was much lower in planted (mean $\pm$ SE: 3.9 ± 2.7 seeds m^{-2}) than in any naturally regenerated stands (22.9 ± 2.1 seeds m^{-2} ; $t = -5.57$, $df = 2.27$, $p = 0.02$; Table S1). Forest structure also varied, as the average height of trees by transect in planted stands was shorter (11.4 ± 0.06 m) than trees in naturally regenerated stands (19.0 ± 1.2 m, $t = -6.04$, $df = 3.02$, $p = 0.009$, Table S2). Serotiny was low in mature lodgepole pines (3% of trees in naturally regenerating stands and 4% in planted stands, Table S2). Seed pressure increased with basal area of live, non-serotinous cone-bearing trees (Spearman’s $\rho = 0.77$, $S = 8$, $p = 0.10$, $n = 6$), yet tree height and cone abundance were unrelated to seed pressure (Table S3). Lodgepole pine seeds comprised $98 \pm 1\%$ of seed collected from seed-pressure transects, consistent with forest composition (Table S2).

Three of the 12 dispersal transects in burned areas trapped no seeds, all adjacent to planted forest stands. For the nine transects that successfully trapped seeds, total lodgepole pine seed delivery was unrelated to live-edge forest characteristics (Table S4). Delivery declined sharply with increasing distance from the live-forest edge, and 64% of seeds were trapped within 20 m (Fig. 4). Seed diversity was low ($94 \pm 5\%$ lodgepole pine), consistent with conifer composition at the live-forest edge (Table S2). Englemann spruce and Douglas-fir seeds were captured in trace amounts (Table S5).

Seed delivery frequency declined linearly with increasing distance in rugged terrain and was higher in rugged than in gentle terrain at distances > 30 m (Table 1, Fig. 5a). In contrast, seed delivery frequency

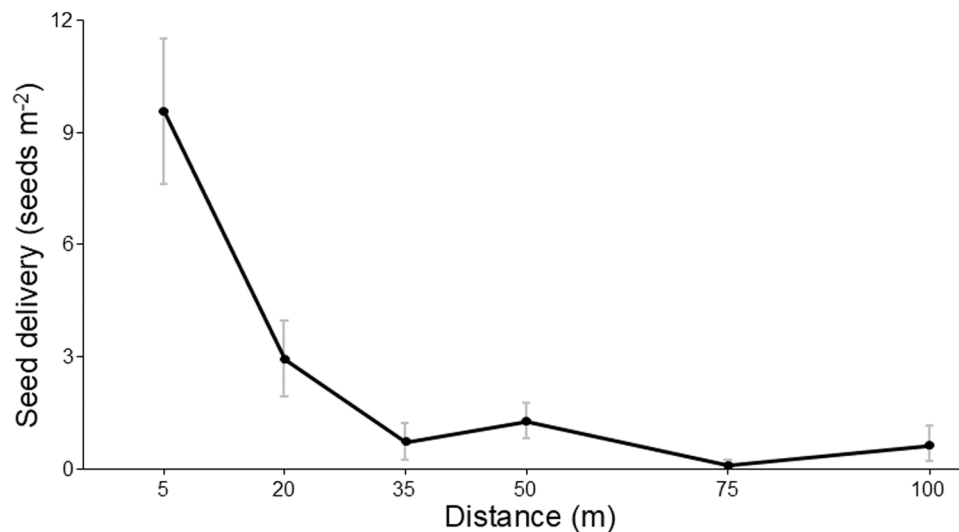


Fig. 4. Mean seed density by distance along the nine transects that successfully trapped seeds. Error bars show ± 1 standard error.

Table 1

Model selection for lodgepole pine seed delivery frequency and density based on transects that successfully trapped seeds ($n = 9$). $\Delta AICc$ represents the difference between a given model and the lowest- $AICc$ model. Distance from the forest edge was included as a predictor for all models. (a) Candidate models for lodgepole pine seed delivery frequency based on GLMs with binomial errors. (b) Candidate models for lodgepole pine seed delivery density, assuming seeds are present. Seed delivery response variables were log-transformed prior to analysis to meet linear model normality assumptions.

a)	Model for lodgepole pine seed delivery frequency	AICc	ΔAICc	df	p	Nagelkerke R ²	
	Frequency ~ distance + ruggedness + distance*ruggedness	60.37	0	50	4.81e-05	0.45	
	Frequency ~ distance	64.71	4.33	52	0.0002	0.30	
	Frequency ~ distance + ruggedness	66.26	5.89	51	0.0007	0.31	
	Frequency ~ distance + orientation	66.51	6.14	51	0.0008	0.31	
	Frequency ~ distance + cone abundance	66.81	6.43	51	0.001	0.30	
	Frequency ~ distance + height	66.93	6.56	51	0.001	0.30	
	Frequency ~ distance + basal area	66.94	6.57	51	0.001	0.30	
	Frequency ~ distance + height + distance*height	67.96	7.59	50	0.002	0.33	
	Frequency ~ distance + basal area + distance*basal area	68.10	7.72	50	0.002	0.32	
	Frequency ~ distance + cone abundance + distance*cone abundance	68.40	8.03	50	0.002	0.32	
b)	Model for lodgepole pine seed delivery density	AICc	ΔAICc	F	df	p	Adjusted R ²
	Delivery ~ distance + ruggedness	37.01	0	33.37	2, 21	3.02e-07	0.74
	Delivery ~ distance + height	40.00	2.99	28.23	2, 21	1.12e-06	0.70
	Delivery ~ distance + basal area	41.91	4.90	25.27	2, 21	2.57e-06	0.68
	Delivery ~ distance	42.20	5.19	43.61	1, 22	1.22e-06	0.65
	Delivery ~ distance + cone abundance	42.76	5.74	24.03	2, 21	3.73e-06	0.67
	Delivery ~ distance + orientation	66.91	29.90	1.43	1, 22	0.24	0.02

declined much more rapidly with distance from the forest edge in gentle terrain, and seed delivery was rare beyond 50 m (Fig. 5a). The odds of trapping lodgepole pine seeds were modeled as:

$$\text{frequency} = 6.24 - 0.19 * \text{distance} - 0.21 * \text{TRI} + 0.01 * \text{distance} * \text{TRI}$$

($p < 0.001$, Nagelkerke $R^2 = 0.45$, Table 1, Table S6a). Transects with higher ruggedness trapped greater seed densities than transects in gentler terrain across the 100 m transect (Table 1, Fig. 5b). Lodgepole pine seed delivery density was modeled as:

$$\log(\text{seed density}) = 1.29 - 0.03 * \text{distance} + 0.04 * \text{TRI}$$

($F = 33.37$, $df = 2, 21$, $p < 0.001$, adjusted $R^2 = 0.74$, Table 1, Table S6b). Transect orientation relative to the live-edge forest (upslope or downslope) and live-edge forest characteristics did not affect seed delivery by distance (Table 1).

3.2. Q2 – Seedling establishment experiment

In lab-based seed viability trials, the proportion of seeds that germinated (i.e. germination rate) was 0.60 for lodgepole pine and 0.78

for Douglas-fir. In the field, however, germination rates were consistently higher for lodgepole pine (mean 0.13 ± 0.03) than for Douglas-fir (mean 0.07 ± 0.03 ; $t = 2.244$, $df = 17.74$, $p = 0.04$; Table S7). All plots had at least one lodgepole pine germinant, whereas Douglas-fir seeds failed to germinate in three rugged plots. Mean germination rates were highest in gentle terrain (lodgepole pine: 0.19 ± 0.05 , Douglas-fir: 0.10 ± 0.05) and lowest in rugged, convex terrain (lodgepole pine: 0.02 ± 0.01 , Douglas-fir: 0.01 ± 0.01 , Fig. S2). More lodgepole pine seeds germinated in concave than convex terrain, and for both species, increasing ruggedness was associated with decreased germination rates (Fig. 6, Table S8). Increasing plot ruggedness was also associated with greater tray damage from soil erosion and cave-ins (Spearman's $\rho = 0.77$, $S = 527.13$, $p < 0.001$, $n = 24$).

The mean proportion of germinants that died the first summer (i.e. mortality rate) did not differ between species (lodgepole pine: 0.83 ± 0.6 , Douglas-fir: 0.86 ± 0.5 , $\chi^2 = 0.006$, $df = 1$, $p = 0.94$, Table S7), but lodgepole pine mortality increased with increasing ruggedness (Spearman's $\rho = 0.50$, $S = 141.89$, $p = 0.09$, $n = 12$). Six of 12 sites had complete lodgepole pine mortality, including plots of all terrain types. Similarly, four of the nine plots with Douglas-fir germinants had no

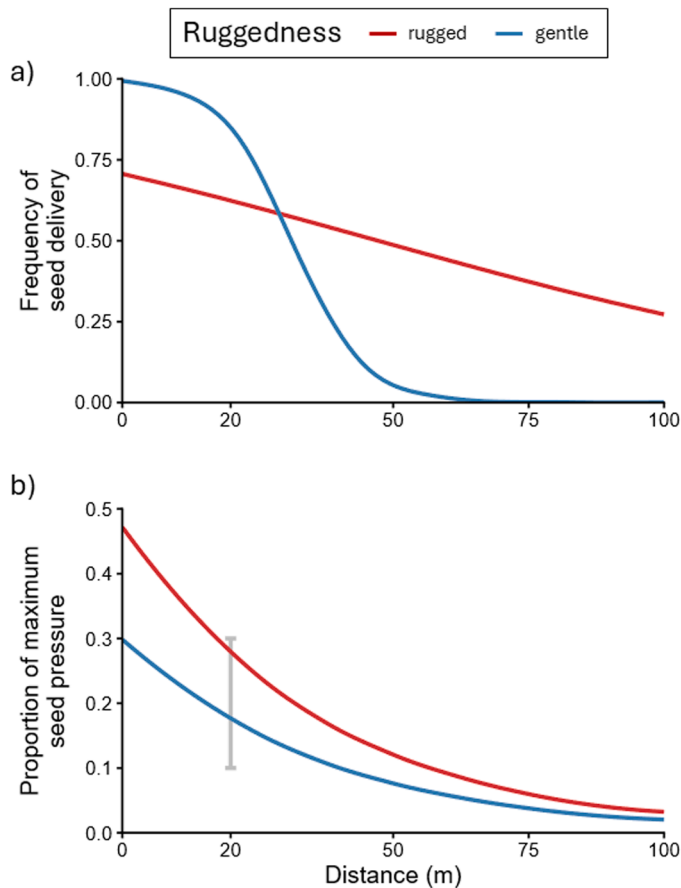


Fig. 5. Modelled effects of rugged (red, TRI > 20.5) and gentle (blue, TRI < 20.5) terrain on lodgepole pine seed dispersal. **(a)** Lodgepole pine seed delivery frequency (i.e. likelihood of seed presence) based on a generalized linear model with binomial errors. **(b)** Lodgepole pine seed delivery density from transects that successfully trapped seeds ($n = 9$), given as a proportion of the maximum observed seed pressure in mature forests (22.5 lodgepole pines seeds m^{-2}). The gray line represents literature estimates (McCaughy et al., 1985) of lodgepole pine seed delivery 20 m from a seed source as a proportion of maximum seed pressure (0.10 – 0.30).

surviving seedlings by the end of the growing season, again including all types of terrain tested. All lodgepole pine germinants died in rugged, convex terrain, but Douglas-fir mortality was lowest in this terrain type. Mean Douglas-fir survival rate in rugged terrain (0.20 ± 0.1) was nearly twice the mean survival rate in gentle terrain (0.11 ± 0.05 , Table S7).

Mean establishment rates (proportion of seeds planted that survived the first summer) for both species were low (lodgepole pine: 0.04 ± 0.02 , Douglas-fir: 0.01 ± 0.01), and five of 12 sites had no establishment of either species by the end of the first growing season (Table S7). Differences in terrain ruggedness and shape did not affect Douglas-fir establishment, while lodgepole pine establishment was lower in rugged terrain (Fig. 6, Table S7). Lodgepole pine seedlings established in six of 12 plots, but establishment in rugged terrain was only successful when the terrain was also concave. Douglas-fir established in five of 12 plots, which included plots of all terrain combinations tested. Means of root and shoot lengths and the ratios of root-to-shoot lengths did not vary between lodgepole pine (root length: 2.93 ± 0.08 cm, shoot length: 1.04 ± 0.04 cm, root-to-shoot: 2.90 ± 0.11) and Douglas-fir (root length: 2.76 ± 0.18 cm, shoot length: 1.03 ± 0.06 cm, root-to-shoot: 3.00 ± 0.42) seedlings. Seedling root-to-shoot ratios did not vary with terrain ruggedness or shape.

3.3. Q3 – Soil microclimate variation

Soil texture in all plots was loamy ($46 \pm 0.53\%$ sand, $35 \pm 0.47\%$ silt, $19 \pm 0.11\%$ clay). Throughout the growing season, soils on concave rugged sites were consistently warmer than soils on gentle or convex rugged plots ($\chi^2 = 35.92$, $df = 3$, $p < 0.001$, Fig. 7). Overall growing season temperatures were warmest in concave rugged ($17.9 \pm 1.0^\circ\text{C}$; mean $\pm$ SE) and concave gentle (concave gentle: $17.3 \pm 1.0^\circ\text{C}$) terrain, while convex plots were slightly cooler (rugged: $17.1 \pm 0.5^\circ\text{C}$, gentle: $16.9 \pm 0.6^\circ\text{C}$). Yet, detrended soil temperature did not statistically differ between terrain ruggedness or shape (Fig. S3, Fig. S10).

Mean soil moisture peaked in early July and late August, with very low soil moisture in between (Fig. 7). Across the growing season, rugged sites were drier than gentle sites, and concave sites were drier than convex ($\chi^2 = 184.47$, $df = 3$, $p < 0.001$, Fig. S4). Mean detrended soil moisture decreased as plot ruggedness increased, meaning plots became drier as they became more rugged ($R^2 = 0.33$, $p = 0.05$, Fig. S5, Table S10).

4. Discussion

Our study revealed strong but contrasting effects of rugged terrain on postfire conifer seed dispersal and establishment, with a tradeoff between enhanced postfire seed delivery and reduced seed germination. The counteracting effects of ruggedness on these processes could produce complex postfire tree regeneration patterns that are not readily explained by distance to seed source. However, relatively small sample sizes due to logistical constraints may have limited our power to detect effects of terrain ruggedness and shape on seedling establishment.

4.1. Seed delivery and diversity

Our results show that rugged terrain facilitated lodgepole pine seed dispersal by increasing both distance traveled and seed density delivered along the dispersal kernel. Wind speed and direction drive seed dispersal (Nathan and Muller-Landau, 2000; Nuttle et al., 2005), and complex terrain can generate variable winds that increase chances of seed uplifting (Bohrer et al., 2008; Katul and Poggi, 2012; Trakhtenbrot et al., 2013; Damschen et al., 2014). Wind patterns in mountainous terrain also vary diurnally as cool air flows downslope in the evenings and warm air rises upslope during the day (Beniston, 2006); thus, seed release timing may affect dispersal magnitude and direction (Greene and Johnson, 1989; Schippers and Jongejans, 2005; Bohrer et al., 2008). Modelling studies suggest wind recirculation on sloped terrain should encourage upslope seed delivery (Trakhtenbrot et al., 2013), yet observational studies of conifer regeneration patterns have reported greater regeneration both downslope (Peeler and Smithwick, 2020; Willson and Hurteau, 2024) and upslope (McCaughy et al., 1985) of live forest patches. Although we did not measure wind speed and direction over the dispersal season, another dispersal study in the GYE found no effect of wind direction on seed delivery (Gill et al., 2021). Diurnal variability and periodic gusts originating from myriad directions suggest seasonal trends in prevailing wind patterns are too coarse to explain seed dispersal patterns in heterogeneous landscapes.

Terrain factors explained substantial portions of the variability in wind-dispersed seed delivery estimates. Literature estimates of lodgepole pine seed delivery 20 m from a forest edge range from 10% to 30% of total lodgepole pine seed pressure within live forest (Lotan and Perry, 1983; Gill et al., 2021). In our model, estimated seed pressure 20 m from the forest edge depended on terrain ruggedness, with delivery of $\sim 17\%$ of lodgepole pine seed pressure expected in gentle terrain and $\sim 28\%$ in rugged terrain. For obligate seeders lacking a seedbank, dispersal potential in gentle terrain is strongly linked to distance from a seed source (Greene and Johnson, 2000; Coop et al., 2010; Hansen et al., 2018; Peeler and Smithwick, 2020), and delivery frequency declines non-linearly with increasing distance (Nathan and Muller-Landau, 2000;

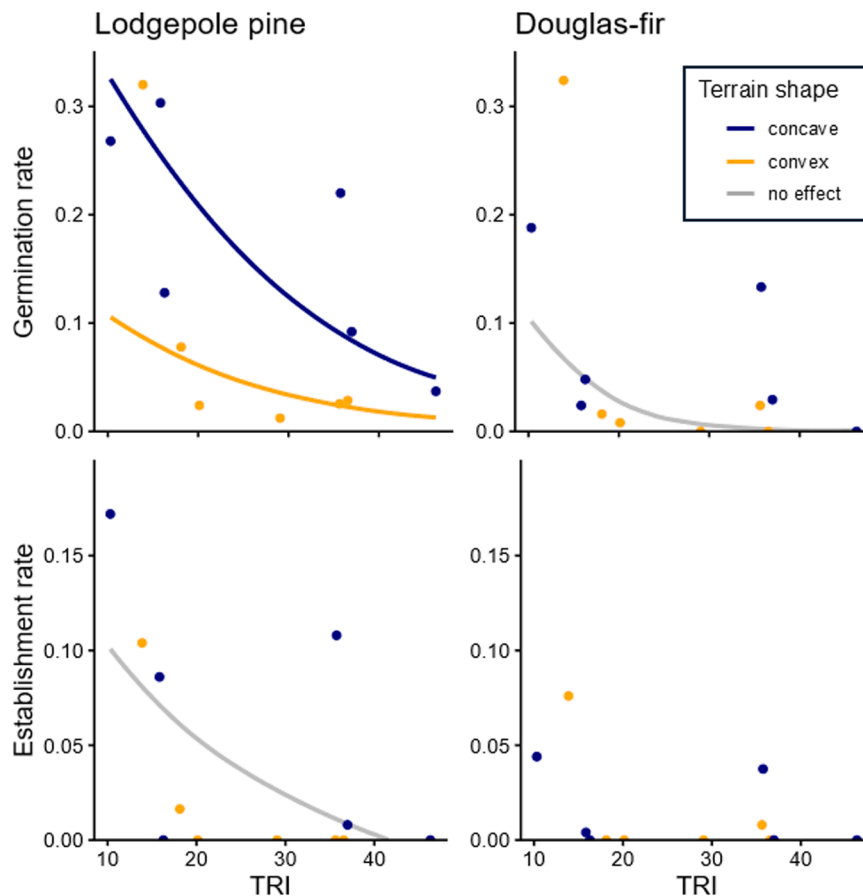


Fig. 6. *In-situ* germination and establishment rates (points) for lodgepole pine (left plots) and Douglas-fir (right plots) with increasing plot TRI (Terrain Ruggedness Index, unitless). Blue and orange curves show model predictions of the additive effects of ruggedness and terrain shape, gray curves show model predictions of effect of ruggedness alone, and no trendline signifies no effect of either ruggedness or shape (Tables S5, S9).

Greene and Johnson, 2000; Nathan et al., 2012). However, seed dispersal in rugged terrain offers an exception to this trend, with delivery frequency declining gently and linearly with distance. Lodgepole pine seeds rarely disperse beyond 60 m (McCaughy et al., 1985; Gill et al., 2021), but we predicted almost twice as much seed delivered at 60 m in rugged terrain (~9% of total seed pressure) compared to gentle terrain (~5%). Based on our model, we expect rugged areas to trap seeds 100 m from a seed source about 27% of the time, comparable to expected seed delivery < 40 m from a seed source in gentle terrain. Thus, greater proportions of disturbed areas in rugged terrain may successfully recruit seeds to support conifer regeneration.

Aside from a close relationship with species composition of seeds, live-edge forest characteristics were not strong predictors of seed dispersal, which is unusual among dispersal studies. Tree height (Greene and Johnson, 1996; Thomson et al., 2011; Gill et al., 2021) and basal area (Greene and Johnson, 2000) are often key parameters for seed dispersal, yet neither were significant predictors in our models, likely due to low variability across study sites because we designed the study around terrain attributes. Our study supports previous literature showing that tree size positively correlates with cone production (Turner et al., 2007; Andrus et al., 2020; Wright et al., 2021; Chybicki et al., 2024), with shorter, planted stands hosting a lower mean cone abundance than the taller naturally regenerated stands.

Our study measured seed pressure during a single season, but results could vary among years because seed production and viability vary in space and time (Shearer, 1985; Gill et al., 2021). For example, seed pressure in planted stands was very low despite the presence of cones, and seed production might be greater in other years. Planted stands also showed evidence of seed and pollen cone predation by small mammals

and a low-intensity surface burn, which were not apparent in any naturally regenerating forest stands but could have reduced seed production or availability. Red squirrels (*Tamiasciurus hudsonicus*), common in our study area, feed on pre-dispersed serotinous and non-serotinous lodgepole pine seeds (Parker and Benkman, 2020) as well as pollen cones in other conifers (Boa-Antwi, 2009), and they can substantially decrease the supply of seeds available for dispersal (Lotan and Perry, 1983). Future work should consider spatial and temporal variability in seed production and predation to avoid overestimating dispersal capacity.

4.2. Seed germination and seedling establishment

Lower lodgepole pine germination rates and higher mortality in rugged than in gentle terrain led to lower lodgepole pine establishment. Concave sites had greater germination; however, this did not translate into a significant effect of terrain shape on establishment due to slight differences in mortality. However, other studies have also shown no effect of terrain shape on lodgepole pine regeneration density, despite its importance for other subalpine conifers (Peeler and Smithwick, 2020). Our results suggest that regeneration mechanisms in complex terrain act in contrasting directions such that increased seed delivery may be negated by decreased establishment, potentially leading to no difference in lodgepole regeneration among terrain types. However, our small sample size may also obscure effects of concave terrain on regeneration.

Douglas-fir germination rates were also lower in rugged than in gentle terrain. However, nonsignificant differences in mortality led to no net effect of ruggedness on Douglas-fir establishment. In contrast to lodgepole pine, terrain shape did not affect germination rates in

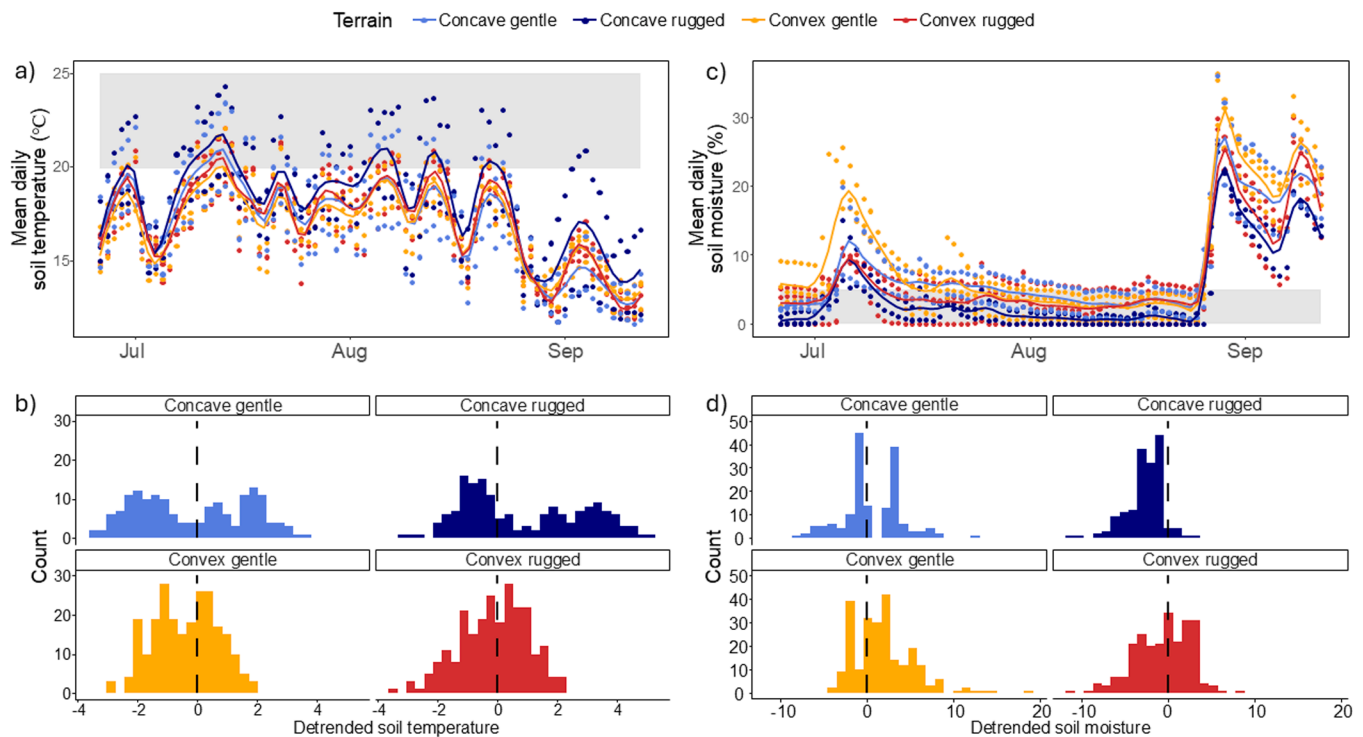


Fig. 7. Mean daily soil temperature (a) and volumetric soil moisture (c). Points show mean daily values for each planting plot and lines represent LOESS model fits by terrain type. Gray boxes represent soil temperature ($>20^{\circ}\text{C}$) and moisture ($<5\%$) values that may limit lodgepole pine and Douglas-fir establishment (Hoecker et al. 2020). Histograms of detrended (i.e. LOESS residuals) mean daily soil temperature (b) and moisture (d) by terrain type.

Douglas-fir. Concave terrain that retains moisture may be less suitable for Douglas-fir germination since this species prefers well-drained soils (Frothingham, 1909; Burns and Honkala, 1990). Because Douglas-fir establishment was low across all sites, it is also possible that we were unable to detect an effect of terrain ruggedness on Douglas-fir establishment.

Germination and establishment rates from our study are similar to other experimental conifer seed sowing experiments in the Rocky Mountains (Hansen and Turner, 2019; Hoecker et al., 2020; Rodman et al., 2025). Differences in germination among terrain types are surprising, as subalpine soils are saturated by snowmelt in the early spring when germination occurs, providing ample moisture to break seed dormancy. For example, a prior experiment in the GYE found no difference in germination among sites that varied in slope aspect, but substantial differences in seedling survival at the end of the growing season (Hoecker et al., 2020). Increased damage from soil erosion and cave-ins in rugged sites explains some of the difference in germination, suggesting terrain conditions may inhibit establishment when slopes exceed a threshold (Kuo et al., 2026).

Installing planting trays and TOMST loggers required flattening seed sowing areas, which may have artificially increased establishment rates. By planting seeds on a flat surface, we ensured that seeds would settle in rugged areas, even when steep slopes may otherwise impede settlement. Likewise, precipitation that would have otherwise run off of steep slopes may have gathered on flattened planting areas, artificially supplementing seedlings with moisture. Seed settlement and germination in un-manipulated rugged areas may be limited to local concavities or sites where woody debris or other plant material prevents post-dispersal seed movement, suggesting that ruggedness at finer scales may also be important for seedling establishment.

4.3. Soil microclimate

Concave rugged sites were warmer and drier across the growing season than other terrain types. Temperature and moisture can control

germination (Kaufmann and Eckard, 1977; Johnson et al., 2011; Urza and Sibold, 2017; Sikder et al., 2025), and rugged sites lost soil moisture more rapidly than gentle sites. Soils in the study region are saturated during snowmelt, but if rugged sites cannot retain moisture throughout the germination period, germination may be reduced or inhibited (Despain, 2001). Precipitation during the germination period was also very low (< 1.25 cm, NWCC, 2026), suggesting low soil moisture may have reduced germination. Similarly, warmer temperatures in rugged areas could affect germination timing and success. Lodgepole pines germinate best when temperatures fluctuate between 8°C and 26°C (Koch, 1996). If rugged sites warm faster than surrounding areas, temperature and moisture windows for optimal germination may be misaligned, thereby shortening the germination window. Similarly, freezing events once germination has begun lowers seedling survival (Hawkins et al., 2003) and may occur if temperature and moisture optima are reached at different times. Daily temperatures recorded at a nearby weather station did not suggest fluctuations above and below freezing during the germination window (NWCC, 2026); thus, we suspect that freeze-thaw cycles did not limit germination.

Warming temperatures can support seedling growth, but seedlings can die if warm temperatures and dry soils exceed tolerance thresholds (Conlisk et al., 2018; Hansen and Turner, 2019). The range of median daily growing season temperatures that support lodgepole pine and Douglas-fir establishment in Yellowstone spans about 5.5°C , (Hansen and Turner, 2019), with higher temperatures putting seedlings at greater risk of desiccation. Thus, the 1°C difference in mean growing season soil temperatures across terrain types may foster less favorable conditions for seedling establishment in rugged areas if increased precipitation cannot compensate for warming temperatures. Annual snowfall is declining in the GYE (Hostetler et al., 2021), and growing season (June – August) precipitation in 2025 (5.8 cm) was substantially lower than historical averages (16.3 cm, NWCC, 2026). Lighter snow-pack causes spring soils to lose moisture rapidly (Andrus et al., 2018), and high wind speeds in rugged terrain can exacerbate moisture stress (Fiedler, 1974; Dobrowski, 2011). Steep slopes and exposed ridges can

also worsen heat stress as poor water retention reduces evaporative cooling potential (Lotan and Perry, 1983). Higher temperatures and decreased moisture in rugged terrain likely combine to lower establishment rates for lodgepole pine and may similarly affect other subalpine species. Terrain shape may counteract some of these effects, as concave sites are expected to have lower minimum temperatures as dense, cold air collects in local elevation minima (Daly et al., 2010; Dobrowski, 2011); however, this process is likely important at larger scales. Instead, we observed higher temperatures in concave terrain, suggesting that these sites may capture solar energy reflected from nearby terrain in addition to direct solar irradiance (Dubayah and Rich, 1995). Warmer and drier rugged areas may become increasingly unsuitable for postfire establishment while valley bottoms and local depressions may retain moisture and support local seedling survival despite warming temperatures (Marsh et al., 2022).

5. Conclusions

Our *in-situ* experiments teased apart mechanisms of postfire conifer regeneration to reveal contrasting effects of seed dispersal and seedling establishment in a topographically complex landscape. Rugged areas enhanced dispersal, which may allow greater proportions of postfire landscapes to receive sufficient seed for forest recovery. However, hotter and drier conditions, greater damage potential, and steep slopes may limit seed settlement and germination in rugged areas. Ruggedness is relevant to regeneration processes at different scales, and broad-scale terrain complexity that enhances dispersal will interact with micro-topography to influence seedling establishment. Our study underscores the importance of experiments to independently assess each stage of a complex process, especially when mechanisms act in contrasting directions to produce landscape patterns.

CRedit authorship contribution statement

Monica G. Turner: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Timon T. Keller:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jillian M. Neece:** Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124145.

Data Availability

Data link provided.

References

- Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci.* 113, 11770–11775.
- Albrich, K., Rammer, W., Seidl, R., 2020. Climate change causes critical transitions and irreversible alterations of mountain forests. *Glob. Change Biol.* 26, 4013–4027.
- Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., Delucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. *Glob. Change Biol.* 19, 2001–2021.
- Andrus, R.A., Harvey, B.J., Rodman, K.C., Hart, S.J., Veblen, T.T., 2018. Moisture availability limits subalpine tree establishment. *Ecology* 99, 567–575.
- Andrus, R.A., Harvey, B.J., Hoffman, A., Veblen, T.T., 2020. Reproductive maturity and cone abundance vary with tree size and stand basal area for two widely distributed conifers. *Ecosphere* 11, e03092.
- Beniston, M., 2006. Mountain weather and climate: a general overview and a focus on climatic change in the Alps. *Hydrobiologia* 562, 3–16.
- Boa-Antwi, K., 2009. Impact of pre-dispersal predation by red squirrels (*Tamiasciurus hudsonicus*) and cone insects on balsam fir (*Abies balsamea*) seed production in eastern Newfoundland. M.S. Memorial University of Newfoundland, St. John's, Newfoundland.
- Boag, A.E., Ducey, M.J., Palace, M.W., Hartter, J., 2020. Topography and fire legacies drive variable post-fire juvenile conifer regeneration in eastern Oregon, USA. *For. Ecol. Manag.* 474, 118312.
- Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L., Avissar, R., 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *J. Ecol.* 96, 569–580.
- Bouyoucos, G.J., 1962. Hydrometer method improved for making particle size analyses of soils. *Agron. J.* 54, 464–465.
- Brown, C.D., Johnstone, J.F., 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *For. Ecol. Manag.* 266, 34–41.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America: Conifers*. U.S. Department of Agriculture, Forest Service, Washington D.C.
- Cansler, C.A., McKenzie, D., 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. *Ecol. Appl.* 24, 1037–1056.
- Chybicki, I.J., Bodziarczyk, J., Meyza, K., Oleksa, A., 2024. Seed production in a dioecious subcanopy conifer tree *Taxus baccata*: the positive effect of neighboring males and female heterozygosity. *Scand. J. For. Res.* 39, 277–286.
- Conlisk, E., Castanha, C., Germino, M.J., Veblen, T.T., Smith, J.M., Moyes, A.B., Kueppers, L.M., 2018. Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of population range shifts. *Glob. Change Biol.* 24, 197–211.
- Coop, J.D., Massatti, R.T., Schoettle, A.W., 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. *J. Veg. Sci.* 21, 472–487.
- Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M.D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A., Fornwalt, P.J., Fulé, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.-A., Prichard, S., Rodman, K.C., 2020. Wildfire-driven forest conversion in western North American landscapes. *BioScience* 70, 659–673.
- Daly, C., Conklin, D.R., Unsworth, M.H., 2010. Local atmospheric decoupling in complex topography alters climate change impacts. *Int. J. Climatol.* 30, 1857–1864.
- Damschen, E.I., Baker, D.V., Bohrer, G., Nathan, R., Orrock, J.L., Turner, J.R., Brudvig, L.A., Haddad, N.M., Levey, D.J., Tewksbury, J.J., 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proc. Natl. Acad. Sci.* 111, 3484–3489.
- Davis, K.T., Higuera, P.E., Sala, A., 2018. Anticipating fire-mediated impacts of climate change using a demographic framework. *Funct. Ecol.* 32, 1729–1745.
- Davis, K.T., Robles, M.D., Kemp, K.B., Higuera, P.E., Chapman, T., Metlen, K.L., Peeler, J.L., Rodman, K.C., Woolley, T., Addington, R.N., Buma, B.J., Cansler, C.A., Case, M.J., Collins, B.M., Coop, J.D., Dobrowski, S.Z., Gill, N.S., Haffey, C., Harris, L.B., Harvey, B.J., Haugo, R.D., Hurteau, M.D., Kulakowski, D., Littlefield, C.E., McCauley, L.A., Povak, N., Shive, K.L., Smith, E., Stevens, J.T., Stevens-Rumann, C.S., Taylor, A.H., Tepley, A.J., Young, D.J.N., Andrus, R.A., Battaglia, M.A., Berkeley, J.K., Busby, S.U., Carlson, A.R., Chambers, M.E., Dodson, E.K., Donato, D.C., Downing, W.M., Fornwalt, P.J., Halofsky, J.S., Hoffman, A., Holz, A., Iniguez, J.M., Krawchuk, M.A., Kreider, M.R., Larson, A.J., Meigs, G.W., Roccaforte, J.P., Rother, M.T., Safford, H., Schaedel, M., Sibold, J.S., Singleton, M.P., Turner, M.G., Urza, A.K., Clark-Wolf, K.D., Yocom, L., Fontaine, J.B., Campbell, J.L., 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. In: *Proceedings of the National Academy of Sciences*, 120.
- De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., Finke, P., Van Meirvenne, M., Verniers, J., Crombé, P., 2013. Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186, 39–49.

- Despain, D.G., 2001. Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. *For. Ecol. Manag.* 141, 59–68.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Change Biol.* 17, 1022–1035.
- Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K., Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. *Glob. Ecol. Biogeogr.* 24, 917–927.
- Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. *Can. J. For. Res.* 39, 823–838.
- Dubayah, R., Rich, P.M., 1995. Topographic solar radiation models for GIS. *Int. J. Geogr. Inf. Syst.* 9, 405–419.
- Fiedler, C.E., 1974. Master of Science, University of Montana. Atmos. Cond. Surround. a seedfall West. Mont.
- Frothingham, E.H., 1909. Douglas fir: A study of the Pacific coast and Rocky Mountain forms. U.S. Department of Agriculture. Forest Service- Circular, p. 150.
- Gill, N.S., Hoecker, T.J., Turner, M.G., 2021. The propagule doesn't fall far from the tree, especially after short-interval, high-severity fire. *Ecology* 102, e03194.
- Gill, N.S., Turner, M.G., Brown, C.D., Glassman, S.L., Haire, S.L., Hansen, W.D., Pansing, E.R., St Clair, S.B., Tomback, D.F., 2022. Limitations to propagule dispersal will constrain postfire recovery of plants and fungi in western coniferous forests. *BioScience* 72, 347–364.
- Greene, D.F., Johnson, E.A., 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70, 339–347.
- Greene, D.F., Johnson, E.A., 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77, 595–609.
- Greene, D.F., Johnson, E.A., 2000. Tree recruitment from burn edges. *Can. J. For. Res.* 30, 1264–1274.
- Hansen, A.J., Phillips, L.B., 2015. Which tree species and biome types are most vulnerable to climate change in the US Northern Rocky Mountains? *For. Ecol. Manag.* 338, 68–83.
- Hansen, W.D., Turner, M.G., 2019. Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. *Ecol. Monogr.* 89, e01340.
- Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a few to tango: Changing climate and fire regimes can cause regeneration failure of two subalpine conifers. *Ecology* 99, 966–977.
- Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94, 2475–2486.
- Harvey, B.J., Donato, D.C., Turner, M.G., 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.
- Hawkins, B.J., Guest, H.J., Kolotelo, D., 2003. Freezing tolerance of conifer seeds and germinants. *Tree Physiol.* 23, 1237–1246.
- Higuera, P.E., Shuman, B.N., Wolf, K.D., 2021. Rocky Mountain subalpine forests now burning more than any time in recent millennia. *Proc. Natl. Acad. Sci.* 118, e2103135118.
- Hijmans, R.J., Brown, A., Barbosa, M., Dyba, K., Bivand, R., Chirico, M., Cordano, E., Pebesma, E., Rowlingson, B., Sumner, M.D., 2026, May 10. Terra. *Spat. Data Anal.*
- Hoecker, T.J., Hansen, W.D., Turner, M.G., 2020. Topographic position amplifies consequences of short-interval stand-replacing fires on postfire tree establishment in subalpine conifer forests. *For. Ecol. Manag.* 478, 118523.
- Hostetler, S., Whitlock, C., Shuman, B., Liefert, D., Drimal, C.W., Bischke, S., 2021. Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds. Montana State University, Institute on Ecosystems, Bozeman MT, p. 260.
- Jacobs, K., Whitlock, C., 2008. A 2000-year environmental history of Jackson Hole, Wyoming, inferred from lake-sediment records. *West. North. Am. Nat.* 68, 350–364.
- Johnson, D.M., McCulloh, K.A., Reinhardt, K., 2011. The Earliest Stages of Tree Growth: Development, Physiology and Impacts of Microclimate. In: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), *Size- and Age-Related Changes in Tree Structure and Function*. Springer Netherlands, Dordrecht, pp. 65–87.
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., Schoennagel, T., Turner, M. G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378.
- Katul, G.G., Poggi, D., 2012. The effects of gentle topographic variation on dispersal kernels of inertial particles. *Geophys. Res. Lett.* 39.
- Kaufmann, M.R., N. Eckard, Alan, 1977. Water potential and temperature effects on germination of Engelmann spruce and lodgepole pine seeds. *For. Sci.* 23.
- Keeley, J.E., Ne'eman, G., Fotheringham, C.J., 1999. Immaturity risk in a fire dependent pine. *J. Mediterr. Ecol.* 1, 41–48.
- Keller, T.T., and M.G. Turner. In press. Rugged terrain may contribute to both resilience and reorganization after wildfire in subalpine forests. *Landscape Ecology*.
- Kemp, K.B., Higuera, P.E., Morgan, P., 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. Northern Rockies. *Landsc. Ecol.* 31, 619–636.
- Kiel, N.G., Turner, M.G., 2022. Where are the trees? Extent, configuration, and drivers of poor forest recovery 30 years after the 1988 Yellowstone fires. *For. Ecol. Manag.* 524, 120536.
- Knowlton, G.J., Keller, T.T., Seidl, R., Turner, M.G., 2025. Simulated postfire tree regeneration suggests reorganization of Greater Yellowstone forests during the 21st century. *Ecosphere* 16, e70415.
- Koch, P., 1996. Lodgepole pine in North America. Forest Products Society, Madison, WI, pp. 1920–1998.
- Kueppers, L.M., Conlisk, E., Castanha, C., Moyes, A.B., Germino, M.J., De Valpine, P., Torn, M.S., Mitton, J.B., 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Glob. Change Biol.* 23, 2383–2395.
- Kuo, C.-C., Liu, Y.-L., Lin, C.-T., 2026. Fine-scale post-fire forest recovery patterns and compound drivers in Taiwan's high-mountain national parks. *For. Ecol. Manag.* 609, 123618.
- Lemon, J., 2006. Plotrix: a package in the red light district of R. R. -N. 6, 8–12.
- Loope, L.L., Gruell, G.E., 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quart. Res.* 3, 425–443.
- Lotan, J.E., Perry, D.A., 1983. Ecology and regeneration of lodgepole pine. U.S. Department of Agriculture Agriculture Handbook.
- Mangiafico, S.S., 2026. rcompanion: Functions to support extension education program evaluation. Rutgers Cooperative Extension, New Brunswick, New Jersey.
- Marsh, C., Krofcheck, D., Hurteau, M.D., 2022. Identifying microclimate tree seedling refugia in post-wildfire landscapes. *Agric. For. Meteorol.* 313, 108741.
- Mazerolle, M.J., 2023. AICcmoDavg: Model selection and multimodel inference based on (QA)IC(c).
- McCaughy, W., Schmidt, W., Shearer, R., 1985. Seed-dispersal characteristics of conifers in the Inland Mountain West.
- McColl-Gausden, S.C., Bennett, L.T., Ababei, D.A., Clarke, H.G., Penman, T.D., 2022. Future fire regimes increase risks to obligate-seeder forests. *Divers. Distrib.* 28, 542–558.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368, eaaz9463.
- Morgan-Wall, T., 2018. rayshader: Create Maps and Visualize Data in 2D and 3D.
- Muir, P.S., Lotan, J.E., 1985. Disturbance history and serotiny of *Pinus contorta* in Western Montana. *Ecology* 66, 1658–1668.
- Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78, 691–692.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. & Evol.* 15, 278–285.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W., Levin, S.A., 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418, 409–413.
- Nathan, R., Klein, E., Robledo-Arnuncio, J.J., Revilla, E., 2012. Dispersal kernels: review. In: Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), *Dispersal Ecology and Evolution*. Oxford University Press, pp. 186–210.
- Nuttall, T., Haefner, J.W., Losos, E.J.B., Loiselle, A.E.B.A., 2005. Seed dispersal in heterogeneous environments: Bridging the gap between mechanistic dispersal and forest dynamics models. *Am. Nat.* 165, 336–349.
- NWCC. 2026. NWCC Report Generator. USDA NRCS. https://wcc.sc.egov.usda.gov/reportGenerator/view/customCalendarYearGroupByMonthReport/monthly/start_of_period/868:WY:SNL%257Cid=%2522%2522%257Cname/1991-01-01,2020-12-31/TAvg:value,PRCP:average,1991?fitToScreen=true
- Parker, A.L., Benkman, C.W., 2020. Enhanced seed defenses potentially relax selection by seed predators against serotiny in lodgepole pine. *Ecol. Evol.* 10, 6001–6008.
- Parks, S.A., Coop, J.D., Davis, K.T., 2025. Intensifying fire season aridity portends ongoing expansion of severe wildfire in Western US forests. *Glob. Change Biol.* 31, e70429.
- Pausas, J.G., Keeley, J.E., 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New. Phytol.* 204, 55–65.
- Peeler, J.L., Smithwick, E.A.H., 2020. Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery. *Landsc. Ecol.* 35, 1945–1959.
- Prichard, S.J., Stevens-Rumann, C.S., Hessburg, P.F., 2017. Tamm Review: Shifting global fire regimes: Lessons from reburns and research needs. *For. Ecol. Manag.* 396, 217–233.
- R Core Team. 2024. R: A language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria.
- Rammer, W., Braziunas, K.H., Hansen, W.D., Ratajczak, Z., Westerling, A.L., Turner, M. G., Seidl, R., 2021. Widespread regeneration failure in forests of Greater Yellowstone under scenarios of future climate and fire. *Glob. Change Biol.* 27, 4339–4351.
- Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermt. J. Sci.* 5, 23–27.
- Rodman, K.C., Veblen, T.T., Battaglia, M.A., Chambers, M.E., Fornwalt, P.J., Holden, Z. A., Kolb, T.E., Ouzts, J.R., Rother, M.T., 2020. A changing climate is snuffing out post-fire recovery in montane forests. *Glob. Ecol. Biogeogr.* 29, 2039–2051.
- Rodman, K.C., Schloegel, C.A., Chapman, T.B., Pineda, M., Chambers, M.E., Fornwalt, P. J., Stevens, J.T., 2025. Give seeds a chance? Opportunities and techniques for post-fire reforestation using tree seeding. *Ecosphere* 16, e70424.
- Schippers, P., Jongejans, E., 2005. Release thresholds strongly determine the range of seed dispersal by wind. *Ecol. Model.* 185, 93–103.
- Schoennagel, T., Turner, M.G., Kashian, D.M., Fall, A., 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. *Landsc. Ecol.* 21, 1281–1296.
- Seidl, R., Turner, M.G., 2022. Post-disturbance reorganization of forest ecosystems in a changing world. *Proc. Natl. Acad. Sci.* 119, e2202190119.
- Shearer, R., 1985. Establishment of conifers following broadcast burning on clearcuts in western Montana (Ph.D.). University of Montana, United States – Montana.
- Sikder, R.K., Biswas, A.K., Iqbal, Md.A., Reza, Md.M., 2025. Seed Germination and Seedling Development in Vegetable Crops. In: Ahammed, G.J., Zhou, J. (Eds.),

- Growth Regulation and Quality Improvement of Vegetable Crops. Springer Nature Singapore, Singapore, pp. 15–50.
- Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.* 21, 243–252.
- Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.* 99, 1299–1307.
- Trakhtenbrot, A., Katul, G.G., Nathan, R., 2013. Mechanistic modeling of seed dispersal by wind over hilly terrain. *Ecol. Model.* 274, 29–40.
- Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol. Monogr.* 67, 411–433.
- Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *Int. J. Wildland Fire* 9, 21–36.
- Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7, 751–775.
- Turner, M.G., Turner, D.M., Romme, W.H., Tinker, D.B., 2007. Cone production in young post-fire *Pinus contorta* stands in Greater Yellowstone (USA). *For. Ecol. Manag.* 242, 119–126.
- Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci.* 116, 11319–11328.
- Turner, M.G., Braziunas, K.H., Hansen, W.D., Hoecker, T.J., Rammer, W., Ratajczak, Z., Westerling, A.L., Seidl, R., 2022. The magnitude, direction, and tempo of forest change in Greater Yellowstone in a warmer world with more fire. *Ecol. Monogr.* 92, e01485.
- Urza, A.K., Sibold, J.S., 2017. Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. *J. Veg. Sci.* 28, 43–56.
- USFS, 2004. Greys River landscape scale assessment. USFS.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open. Source Softw.* 4, 1686.
- Wild, J., Kopecký, M., Macek, M., Sanda, M., Jankovec, J., Haase, T., 2019. Climate at ecologically relevant scales: a new temperature and soil moisture logger for long-term microclimate measurement. *Agric. For. Meteorol.* 268, 40–47.
- Willson, K.G., Hurteau, M.D., 2024. Abiotic factors modify ponderosa pine regeneration outcomes after high-severity fire. *Ecosystems* 27, 606–620.
- Wright, M.C., Van Mantgem, P., Stephenson, N.L., Das, A.J., Keeley, J.E., 2021. Seed production patterns of surviving Sierra Nevada conifers show minimal change following drought. *For. Ecol. Manag.* 480, 118598.