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The propagule doesn't fall far from the tree, especially after short-interval, high-severity fire

NATHAN S. GILL,[1,2] TYLER J. HOECKER, AND MONICA G. TURNER

Department of Integrative Biology, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, Wisconsin 53706 USA

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Abstract. Subalpine forests that historically burned every 100–300 yr are expected to burn more frequently as climate warms, perhaps before trees reach reproductive maturity or produce a serotinous seedbank. Tree regeneration after short-interval (<30-yr) high-severity fire will increasingly rely on seed dispersal from unburned trees, but how dispersal varies with age and structure of surrounding forest is poorly understood. We studied wind dispersal of three conifers (*Picea engelmannii*, *Abies lasiocarpa*, and *Pinus contorta* var. *latifolia*, which can be serotinous and nonserotinous) after a stand-replacing fire that burned young (≤30 yr) and older (>100 yr) *P. contorta* forest in Grand Teton National Park (Wyoming, USA). We asked how propagule pressure varied with time since last fire, how seed delivery into burned forest varied with age and structure of live forest edges, what variables explained seed delivery into burned forest, and how spatial patterns of delivery across the burned area could vary with alternate patterns of surrounding live forest age. Seeds were collected in traps along 100-m transects ($n = 18$) extending from live forest edges of varying age (18, 30, and >100 yr) into areas of recent (2-yr) high-severity fire, and along transects in live forests to measure propagule pressure. Propagule pressure was low in 18-yr-old stands (~8 seeds/m^2) and similarly greater in 30- and 100-yr-old stands (~32 seeds/m^2). Mean dispersal distance was lowest from 18-yr-old edges and greatest from >100-yr-old edges. Seed delivery into burned forest declined with increasing distance and increased with height of trees at live forest edges, and was consistently higher for *P. contorta* than for other conifers. Empirical dispersal kernels revealed that seed delivery from 18-yr-old edges was very low (≤2.4 seeds/m^2) and concentrated within 10 m of the live edge, whereas seed delivery from >100-yr-old edges was >4.9 seeds/m^2 out to 80 m. When extrapolated throughout the burned landscape, estimated seed delivery was low (<49,400 seeds/ha) in >70% of areas that burned in short-interval fire (<30 yr). As fire frequency increases, immaturity risk will be compounded in short-interval fires because seed dispersal from surrounding young trees is limited.

Key words: *dispersal kernel; Engelmann spruce; fire frequency; fire-regime change; forest structure; Greater Yellowstone Ecosystem; lodgepole pine; resilience; seed dispersal; subalpine fir.*

INTRODUCTION

Climate warming is increasing fire frequency and annual area burned across much of the western United States (Westerling et al. 2006, Abatzoglou and Williams 2016) and in many forest ecosystems around the world (Flannigan et al. 2009, Prichard et al. 2017). Understanding the effect of short-interval, high-severity fires on postfire vegetation dynamics and recovery is a key priority for contemporary fire ecology research (Prichard et al. 2017). Postfire regeneration of obligate seeders can be reduced after short-interval high-severity fires (Brown and Johnstone 2012, Turner et al. 2019), but the relative importance of seed dispersal as a control of postfire tree regeneration after short-interval fire in young forests is not clear.

Even species that are evolutionarily fire adapted may be sensitive to shifts in fire frequency when rates of burning depart from historical ranges of variability (Buma et al. 2013). For example, immaturity risk in serotinous species arises when a second fire burns before trees have reached reproductive maturity and developed a canopy seedbank (Keeley et al. 1999). Soil seedbanks of tree species are not present in these systems (Turner et al. 1994, Johnson and Fryer 1996), and thus all seed after stand-replacing fire must come either from serotinous cones, within-patch survivors, or seed sources outside of burned patches. A single *Pinus contorta* tree becomes sexually mature at 5–15 yr of age (Clements 1910, Wheeler and Critchfield 1985), and even in serotinous individuals, initial cones are nonserotinous (e.g.,

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[1] Current address: Department of Natural Resources Management, Texas Tech University, Goddard Building, Box 42125, Lubbock, Texas 79409 USA

[2] E-mail: nathan.gill@ttu.edu

Turner et al. 2007); the proportion of cones that are serotinous increases with age (Lotan 1976). Serotiny is a genetically controlled trait believed to be selected by past fire histories (Lotan 1976, Schoennagel et al. 2003, Parchman et al. 2012). Individual serotinous cones may be produced within the first 2–3 decades after establishment, but a serotinous seedbank can take several decades beyond sexual maturity to develop fully (Lotan 1976). *Pinus contorta* may hold serotinous cones and viable seeds for 80 yr or more (Bradley et al. 1992). Effects of reduced seed supply may be amplified by a warming and drying climate, which can reduce growth, survival, and fecundity in woody plants, effectively lengthening the time required to reach reproductive maturity in places where intervals between fires are also decreasing (i.e., interval squeeze; Enright et al. 2015). Seed dispersal from sources outside of burned patches will be increasingly important under more frequent fire in systems where serotiny has been important historically.

For species that rely on seed dispersed from mature, live trees in surrounding unburned forest, the dispersal process may also be sensitive to novel landscape patterns expected to arise as fire regimes change. Dispersal processes limit postdisturbance tree establishment in a wide range of forests (Greene et al. 1999, Greene and Johnson 2000, Despain 2001, Albani et al. 2005, Tautenhahn et al. 2016). Although seed-release height is an important determinant of dispersal distance (Greene and Johnson 1989, 1996, Nathan et al. 2001), studies to date have primarily focused on height differences of mature plants rather than differences among age classes (Thomson et al. 2011, Tamme et al. 2014). Ergo, simulation models often assume a single dispersal kernel for a given species, ignoring variability in live forest structure. Under historical fire regimes, live subalpine forest edges were primarily dominated by mature forest. Thus, modeling dispersal variability by forest age and structure may have been unnecessary before the onset of rapid change in fire regimes. This applies not only to subalpine forests, but to any forest in which increased fire frequency may alter the height of trees surrounding patches of stand-replacing disturbance. Models suggest that distance to seed source following short-interval fires will be a critical determinant of forest resilience (the ability to recover to a similar state after disturbance) under future climate (Hansen et al. 2018), but the effects of increased fire frequency on the dispersal range of many species, including lodgepole pine (*P. contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), have not been empirically tested.

In addition to seed-release height, wind dispersal is also sensitive to factors that influence wind speed and direction. For example, dispersal from the windward side of a clear-cut area can be expected to reach farther into a patch than from the leeward side (Greene and Johnson 1996). Topography and forest structure can also influence wind turbulence, affecting patterns of seed dispersal (Greene and Johnson 1996, Damschen et al. 2014). *Picea engelmannii* and *Abies lasiocarpa* (both nonserotinous species) are obligate seeders that codominate much of the Rocky Mountains. Although their seeds may also be dispersed by animals (Lanner 1983, Alexander 1987), they are primarily dispersed by wind, reaching distances of up to 80 m (Noble and Ronco 1978) when released from old, tall trees.

The aims of this study were to answer four questions pertaining to seed dispersal of three conifer species (*P. contorta* var. *latifolia*, *P. engelmannii*, and *A. lasiocarpa*) 2 yr after stand-replacing fire (i.e., killing all or most trees, thus making stand age synonymous with time since last fire; Romme and Despain 1989, Millspaugh et al. 2000). We asked (1) How do forest structure, cone abundance, and propagule pressure within live forests vary with stand age? (2) How does total seed delivery into high-severity burned forest vary with age of surrounding live forest edge? (3) What predictors (including forest structure, wind, and topography) best explain patterns of seed delivery in a postfire, *P. contorta*–dominated landscape? (4) How might increased prevalence of young (≤30-yr-old) forest alter spatial patterns of seed delivery throughout a burned landscape?

We expected that propagule pressure would increase with stand age; that total seed delivery into burned areas would be greater from older, taller trees, with greater cone abundance, with greater wind speeds, and at shorter distances from live edges; and that total seed delivery into burned areas would be limited where surrounding forest was young. We expected that *A. lasiocarpa* and *P. engelmannii* seeds would disperse farther into burned patches than *P. contorta* seeds (Shearer 1986, Burns and Honkala, 1990), but that there would be relatively more *P. contorta* seeds because of the dominance of *P. contorta* in these young, postfire forests. We also thought that the density of fire-killed snags could either impede dispersal (as physical barriers) or enhance dispersal (by increasing turbulence; Nathan et al. 2002, Damschen et al. 2014).

Methods

Study area

This study was conducted in subalpine forests in Grand Teton National Park (northwest Wyoming, USA) that burned at high severity in the 2016 Berry Fire (Fig. 1). Prior to 2016, vegetation cover was dominated by stands of young *P. contorta* that regenerated after recent fires, as well as older mixed stands of *P. contorta*, *P. engelmannii*, and *A. lasiocarpa*. Each of these conifer species flowers in May–July and releases the majority of seeds between August and October (Liu 1971, Lotan and Perry 1983, Alexander et al. 1986, Alexander 1987). The elevation of the study area ranges from 2,000 to 2,800 m above sea level (asl). Mean annual precipitation averages 77.0 cm of rainfall and 643.9 cm of snow.

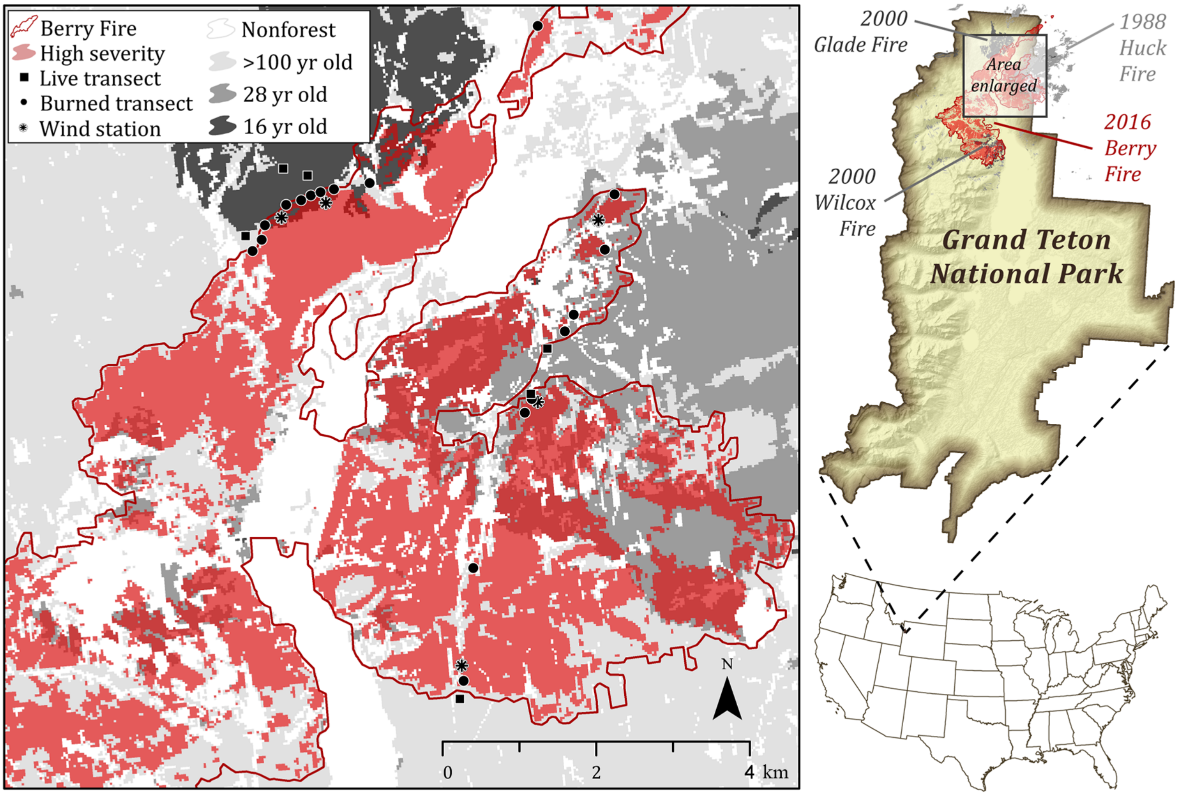

FIG. 1. Study area. This study was conducted within the 4,340-ha area that burned at high severity (i.e., stand-replacing fire) in the 2016 Berry Fire in Grand Teton National Park, Wyoming, USA. Ages given here are at time of fire, 2 yr before data collection.

Temperatures range from an average minimum of −17.7°C in January to an average maximum of 25.3°C in July (Snake River station, Wyoming; Western Regional Climate Center, accessed 9 April 2019). Soils are derived from underlying rhyolitic or andesitic bedrock. These forests have historically burned in large, high-severity crown fires occurring every 100–300 yr (Millspaugh et al. 2000). However, recent fires in the region have reburned young postfire forests (Turner et al. 2019), a phenomenon expected to become more common as climate warms (Westerling et al. 2011, Liu et al. 2013). Of the ~8,500 ha area that burned in the Berry Fire, 4,340 ha burned at high severity, including 648 ha that reburned 28-yr-old forest (regenerated after the 1988 Huck Fire) and 294 ha that reburned 16-yr-old forest (regenerated after the 2000 Glade and Wilcox fires).

Field methods

Stand structure and cone abundance were measured along 50 × 2 m *live-edge plots* ($n = 18$; Appendix S1: Fig. S1) stratified by age of live forest (18-yr-old [$n = 5$], 30-yr-old [$n = 6$], and >100-yr-old [$n = 7$]; Fig. 2) at the edge of the burn, set 5 m inside the live forest (see Appendix S1: Table S1). Transect locations were randomly selected from areas within 4.0 km of a road, stratified by age class of live forest edge. At 2-m intervals in each live-edge plot, the species, height, diameter at 1.4 m, and cone abundance category of the nearest live, cone-bearing tree were recorded ($n = 25$). Cone abundance was classified as <10, 10–50, 51–100, or >100 cones per tree. Each tree was also scored for the presence of at least one serotinous cone, and stand serotiny was calculated as a percent of live, cone-bearing trees. Serotinous *P. contorta* cones can be visually distinguished from mature nonserotinous cones because they are sealed, held at an acute angle to the limb, and are morphologically distinct. Immature cones (≤2 yr old), for which serotiny cannot be definitively ascribed, were not counted as serotinous cones. Cone maturity was estimated by the number of whorls on a tree limb. Finally, the number of live, cone-bearing trees within the live-edge plot was tallied by species.

Seed delivery into the recently burned forest was measured along 100-m *burned seed delivery transects* ($n = 18$) running perpendicular from the midpoint of each *live-edge plot* into the burn (Appendix S1: Fig. S1). Within each age class (18-yr-old, 30-yr-old, and >100-yr-old), transects were widely spaced throughout the large Berry Fire to capture variation in topographic position and direction relative to prevailing winds (Appendix S1: Table S1); the closest transects were

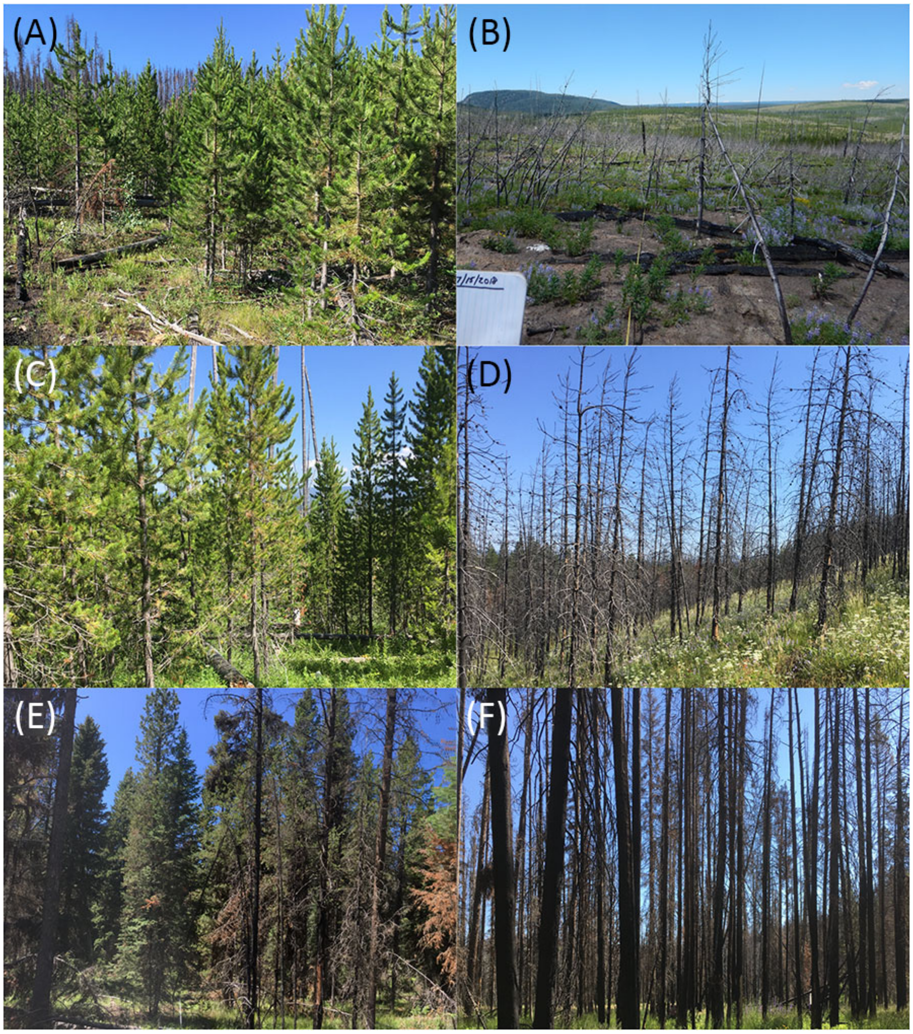

FIG. 2. Three different age classes of forest that burned in the Berry Fire, with unburned counterparts. Burned (right) and unburned, live forest edges (left) of varying-age *Pinus contorta*–dominated stands in Grand Teton National Park, USA. Stand age is determined by time since last fire, due to the stand-replacing nature of fires in this system. (A–B) 18-yr-old forest. (C–D): 30-yr-old forest. (E–F): >100-yr-old forest.

separated by >150 m. Starting at the live forest edge, two 0.28 × 0.54 m trays (6.20 cm deep) were placed at 1-, 5-, 10-, 20-, 30-, and 40-m positions along each transect into the burned forest (Appendix S1: Fig. S1). Four trays were placed at 50 m along each burned transect and eight trays were placed at 100 m, to account for decreased likelihood of capturing seeds at greater distances (Nathan et al. 2000*a*). Trays were left in place for the duration of the dispersal season (July–October 2018). Trays were covered by 0.635-cm^2 grain hardware cloth, large enough to allow conifer seeds to enter but fine enough to prevent seed removal by birds and rodents. Landscaping fabric was placed in the bottom of trays to retain seeds while allowing water to drain from slits in tray bottoms. Hereafter, a set of trays at a single interval along a transect is referred to as a "seed trap," composed of 2–8 trays. The number of standing dead trees (snags) within 1 m of either side of burned transects was measured over the first 50 m to estimate snag density. The slope of each transect was recorded using a clinometer.

Baseline propagule pressure deep within live forests was also measured over 3 months at six randomly located sites stratified by age class. Presumably, this represents an estimate of the upper limit of seed delivery that could be achieved from edges of each age class. Understanding propagule pressure provides important context for interpreting the seed delivery values measured in burned areas. At each site, one tray was placed every 2 m along a 50-m *propagule pressure transect* (Appendix S1: Fig. S1) in July 2018 (n = 24 trays per site).

Wind speed and direction data were recorded at 30-min intervals over the 3.5 months of seed trapping using METER Environment meteorological stations ($n = 5$). Data from the nearest station were attributed to each transect (no farther than 2.7 km away).

Contents of all intact seed traps in live and burned forest were collected 15–21 October 2018, and *P. contorta*, *P. engelmannii*, and *A. lasiocarpa* seeds were counted in a laboratory. Seed-delivery data were square-root transformed prior to analysis to meet modeling assumptions of normalized variance.

Analysis

Forest structure, cone abundance, and propagule pressure (Question 1).—Differences among forest age classes in the density, diameter, and height of live cone-bearing trees, along with cone abundance and presence of serotinous cones, were evaluated using the Kruskal–Wallace test ($n = 18$). Propagule pressure within live forest of each age class was measured by tree species for each propagule pressure transect ($n = 6$).

Total seed delivery (Question 2).—The sum of seeds captured in the eight traps was determined by species for each live and burned transect, other than one 30-yr-old burned transect that had five of its eight traps compromised by tipping or breakage, presumably by wildlife. Analysis of variance (ANOVA) was used to determine whether total seed delivery varied by age class.

Variables explaining P. contorta *seed dispersal (Question 3).*—Using the R package lmerTest version 3.0-1 (Kuznetsova et al. 2017), we then fit mixed-effects models to estimate *P. contorta* seed delivery into burned areas, with transect as a random variable in all models and log of distance (Greene and Johnson 2000) as a fixed effect in any model that considered distance. This negative exponential transformation was selected from among many possible kernel models (Clark et al. 1999, Nathan et al. 2000b, Tautenhahn et al. 2012) based on the literature concerning the species of interest (Noble and Ronco 1978, Greene and Johnson 1989, 2000) as well as the visual interpretation of our data.

Distance, age class, tree height, cone abundance, wind direction, snag density, and topographic slope were included as fixed-effect predictors of seed delivery in an exhaustive model selection procedure (Appendix S1: Table S2). These candidate predictors were tested for collinearity and collinear variables were never included in the same model. Working backward from each possible combination of all noncollinear variables, the most important predictors were identified through comparison of Nagelkerke's R^2 (Nagelkerke 1991). Models of different complexities were then compared through Akaike information criterion (AIC; we established an a priori threshold of 2 AIC units, but no other models were within 7 AIC units of the selected model). The strongest model based on AIC and Nagelkerke R^2 was selected for formulating the dispersal kernel and making spatial estimates of *P. contorta* seed delivery. No model was selected for *P. engelmannii* nor for *A. lasiocarpa*, because seed delivery (and thus, explanatory power) was low.

Forest age and spatial patterns of postfire seed delivery (Question 4).—*Pinus contorta* seed delivery within the whole study area was projected using the selected empirical model and the current age–class distribution of postfire forests. The formula from the selected model was backtransformed (i.e., squared to return the metric to its original scale) and applied to the study area in a GIS (ArcGIS 10.6), using distance from live forest edges and the mean tree height of each age class. These distances were determined by calculating Euclidean distance over a grid of 10 × 10 m pixels representing the burned area (Appendix S1). We then used the same process to project seed delivery into the burned area assuming that all surrounding forest was 30 and, separately, 18 yr old. These scenarios represent simplified potential future conditions that could become more common as fire frequency in the Greater Yellowstone Ecosystem (GYE) increases.

To evaluate whether seed supply and dispersal had the potential to limit forest recovery, we evaluated the predicted seed delivery patterns against stem density criteria that could be used as indicators of forest recovery. A wide variety of definitions exist for the minimum amount of tree cover to qualify as "forest cover" (Chazdon et al. 2016). To interpret our estimates of seed delivery following the 2016 Berry Fire given actual age structure and under the two young-forest scenarios, we delineated areas where seed delivery became insufficient to meet three different tree-density threshold definitions (Appendix S1: Table S3). Annual seed delivery was converted to potential stem density by multiplying by an empirically derived seed-to-seedling ratio (0.01; Vyse and Navratil 1958, Koch 1987), and then multiplied by 3 to represent 3 yr during which abundant mineral soil coverage is conducive to *P. contorta* colonization following high-severity fire (Alexander 1974). These estimates are not meant to predict future forest cover, but rather to explore the potential for seed delivery to constrain future forest cover. Future forest cover will also depend on altered rates of germination and establishment, survival and growth of juveniles, and the seed delivery of other tree species, such as aspen, which were not considered here. We note that these factors may also vary with distance from live forest edge, though incorporating them is beyond the scope of the current study. As such, these estimates err on the side of overestimating future *P. contorta* cover, and should be interpreted accordingly.

RESULTS

Live-edge structure, cone abundance, and propagule pressure

Structural attributes of live forest edges and cones per tree varied by age class, but stand-level cone abundance did not (Appendix S1: Table S4). The density of live cone-bearing trees was greatest in the 18-yr age class (7,080 stems/ha) and declined to 3,600 and 1,670 stems/ha in the 30- and >100-yr-old age classes, respectively (Appendix S1: Fig. S2A). Tree height (and similarly, diameter) increased with stand age Appendix S1: (Fig. S2B, C), with trees averaging ~12 m in height in the >100-yr old age class, ~6 m in the 30-yr-old class, and ~3 m in the 18-yr-old class. The number of cones on individual live cone-bearing trees increased with stand age (Appendix S1: Fig. S2D), but stand-level cone density was similar among stand ages (Appendix S1: Fig. S2E, Table S4). Only live forest edges >100 yr old contained cone-bearing trees of *P. engelmannii* and *A. lasiocarpa* (Appendix S1: Table S5), and *P. contorta* represented 81 ± 8% of cone-bearing trees in these older forests (Appendix S1: Fig. S2F, Table S6). On 18-yr-old trees, nearly all cones were nonserotinous, and the proportion of trees holding any serotinous cones ranged from 0% to 28%. At >100-yr-old edges, serotinous trees often held >100 cones and the proportion of serotinous trees ranged from 0% to 41%.

Pinus contorta propagule pressure in live forests was low in the 18-yr-old age class (8.2 seeds/m^2) and greater (but similar to each other) in the 30- and >100 yr-old age classes (35.0 and 29.2 seeds/m^2, respectively). *Pinus contorta* accounted for nearly all seed in the two younger age classes and 80% of seed in the older stands (Appendix S1: Table S7). *Picea engelmannii* propagule pressure was estimated (from the mean) at 0.6, 1.4, and 2.7 seeds/m^2 within 18-, 30-, and >100-yr-old age classes, respectively (Appendix S1: Table S7). *Abies lasiocarpa* propagule pressure was estimated at 0.3, 0.3, and 5.3 seeds/m^2 within 18-, 30-, and >100-yr-old age classes, respectively (Appendix S1: Table S7).

Patterns of seed delivery into burned forest

Seventy-seven percent of traps across all age classes and distance intervals into burned forest collected *P. contorta* seeds (Appendix S1: Table S8). Sixty-one percent of traps collected *P. engelmannii* and 17% captured *A. lasiocarpa*, with traps at many distance intervals capturing no seeds of either of these two species in the younger age classes (Appendix S1: Table S8).

Seed delivery of each species decreased with distance from live forest edge and was highest when adjacent live edges were >100 yr old (Fig. 3; Appendix S1: Tables S9–S11). When live-edge forests were >100 yr old, *P. contorta* seed delivery exceeded 10 seeds/m^2 for at least 30 m, then declined gradually (Fig. 3A). When live-edge forests were 30 yr old, mean *P. contorta* seed delivery declined below 10 seeds/m^2 within 10 m. Mean *P. contorta* seed delivery was consistently low (<10 seeds/m^2) when live forests were 18 yr old (Fig. 3A), even near edges. Total (sum of entire transect) *P. contorta* seed delivery was higher from >100-yr-old edges than from 18-yr-old edges (10.2 and 2.8 seeds/m^2, respectively;

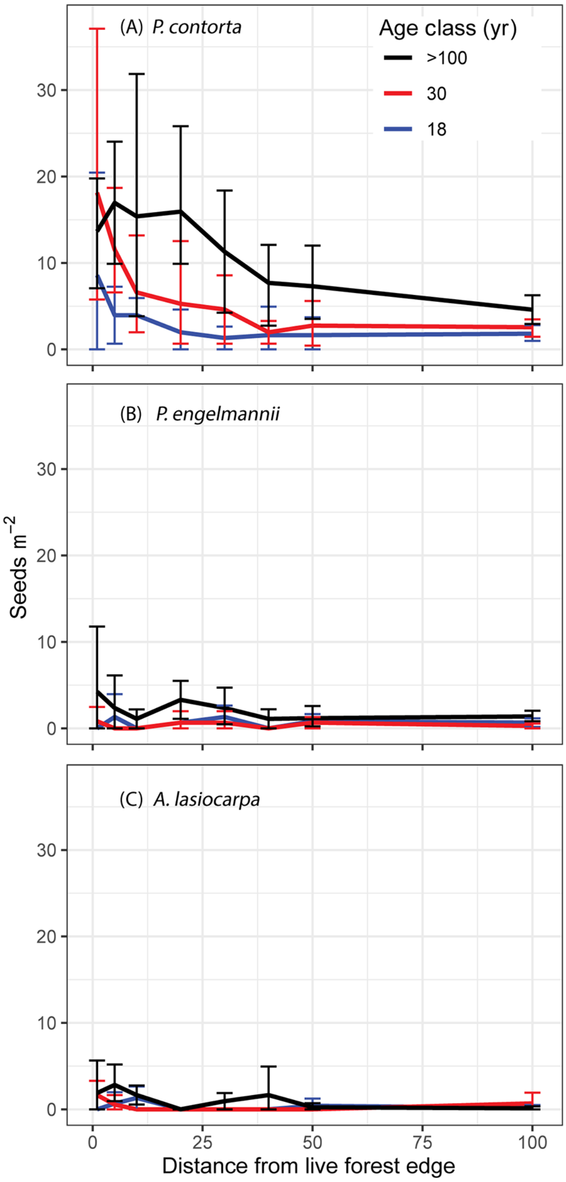

FIG. 3. Seed delivery over distance into burned forest from live forest edge, by age class. Age classes were a natural result of time since last fire: 18 yr ($n = 5$), 30 yr ($n = 6$), or >100 yr ($n = 7$). Error bars represent bootstrapped confidence intervals at the 95% level.

ANOVA $F = 5.144$, $P = 0.0211$). Total *P. contorta* seed delivery from 30-yr-old edges did not differ from either of the other age classes. *Picea engelmannii* and *A. lasiocarpa* total seed deliveries were low even when adjacent live edges were >100 yr old (Fig. 3B, C). *Picea engelmannii* and *A. lasiocarpa* seeds were too sparse to test for differences by age class under the assumptions of ANOVA.

Drivers of P. contorta seed dispersal into burned forest

Postfire *P. contorta* seed delivery into burned forest was best predicted by distance from and height of the adjacent live forest edge (Table 1). The dispersal kernel of *P. contorta* seed into burned areas was modeled as

$$k_{pc} = (-0.0575 \times \log(d) + 0.0258h + 0.2813)^2$$

where k denotes the proportion of seeds (compared to maximum observed seed delivery under live canopies) delivered at distance d (m) given live cone-bearing tree height h (m) ($R^2 = 0.45$). This is the formulaic representation of the mixed-effect model that we found to be strongest in our analysis of empirical seed delivery data, holding random effects constant and transforming the predicted response back to its original scale by squaring it. This model better predicted seed delivery and explained more variance than models that included age cone abundance, topography, transect alignment with prevailing winds, or snag density (Table 1). Snag density and age class each also produced a significant model, but each was a less powerful predictor and was closely correlated with tree height ($r = -0.61$). Thus, they were not included in the same model. *Pinus contorta* dispersal kernels varied by age class because of differences in height, and seed delivery into the burned area was substantially lower from younger edges (Fig. 4).

TABLE 1. Models explaining *Pinus contorta* seed delivery into areas of high-severity fire that had burned 2 yr previously.

Independent variables used	Nagelkerke R^2	t	P
Height and distance	**0.4474**	**6.269**	**<0.0001**
Age and distance	**0.3867**	**3.214**	**0.0056**
Topographic slope and distance	0.3425	−0.131	0.8970
Wind direction and distance	0.3568	−1.649	0.1190
Snag density and distance	**0.3828**	**−3.010**	**0.0085**
Cone abundance and distance	0.3553	1.559	0.1380

Notes: Each of these models included the natural log of distance from live edge and one additional independent variable, as indicated. Seed-delivery data were square-root transformed. Bold type indicates significance at the 0.05 level.

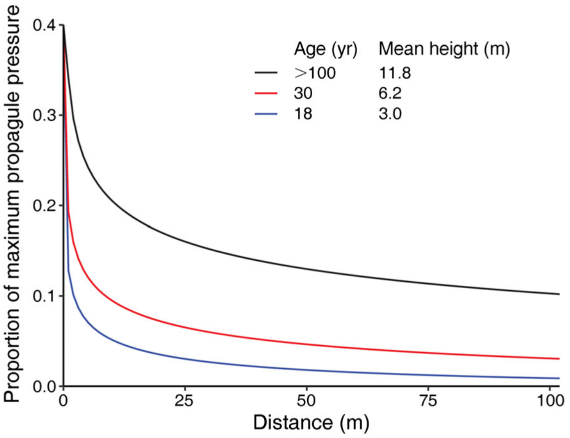

FIG. 4. *Pinus contorta* dispersal kernel given mean stand height by age class. Proportion of maximum propagule pressure is the ratio of seeds/m^2 compared to maximum observed seed delivery within surrounding live forest.

Projected spatial patterns of postfire seed delivery throughout study area

Given the current age structure of surrounding forest, estimated seed delivery averaged 54,600 seeds/ha and varied from 20,600 to 94,000 seeds/ha (Fig. 5A; Appendix S1: Fig. S3A). Even at the most distant locations from live edges, estimated seed delivery exceeded all but the most stringent of the forest cover thresholds we considered (49,400 annual seeds/ha; Appendix S1: Table S3; Alexander, 1974). In total, 54% (2,360 ha) of the stand-replacing burn was predicted to receive seed sufficient to exceed that threshold (Table 2). However, the areas with estimated seed delivery below the threshold all occurred in young reburned forest or in the centers of large burned patches (Fig. 5A, Appendix S1: Fig. S3A; see also Fig. 1). Of the 942 ha of ≤30-yr-old forest that burned in the Berry Fire, 74.2% (699 ha) fell below the 49,400 seed ha^{-1} threshold (Table 2). Estimated seed delivery was higher in portions of the landscape where many smaller patches of old forest remained after fire (where the burn-severity mosaic was most spatially heterogeneous; Appendix S1: Fig. S3A). Even areas of young reburned forest were estimated to have sufficient seed delivery if burned patches were small and older live forest was nearby (Appendix S1: Fig. S3A).

Under the scenario in which the entire live edge was 30 yr old, projected annual *P. contorta* seed delivery averaged 21,700 seeds/ha across the entire study area and varied from 2,800 to 43,400 seeds/ha (a total reduction of 60.3% compared to estimates using the actual age structure). None of the study area would meet the highest seed delivery threshold for recovery under this scenario (Alexander 1974), and only 70% of the study area would receive sufficient seed to meet the moderate threshold of 14,100 seeds/ha (Appendix S1: Table S3). However, the entire area would receive >1,700 seeds/ha (Table 2, Fig. 5B; Appendix S1: Fig. S3B).

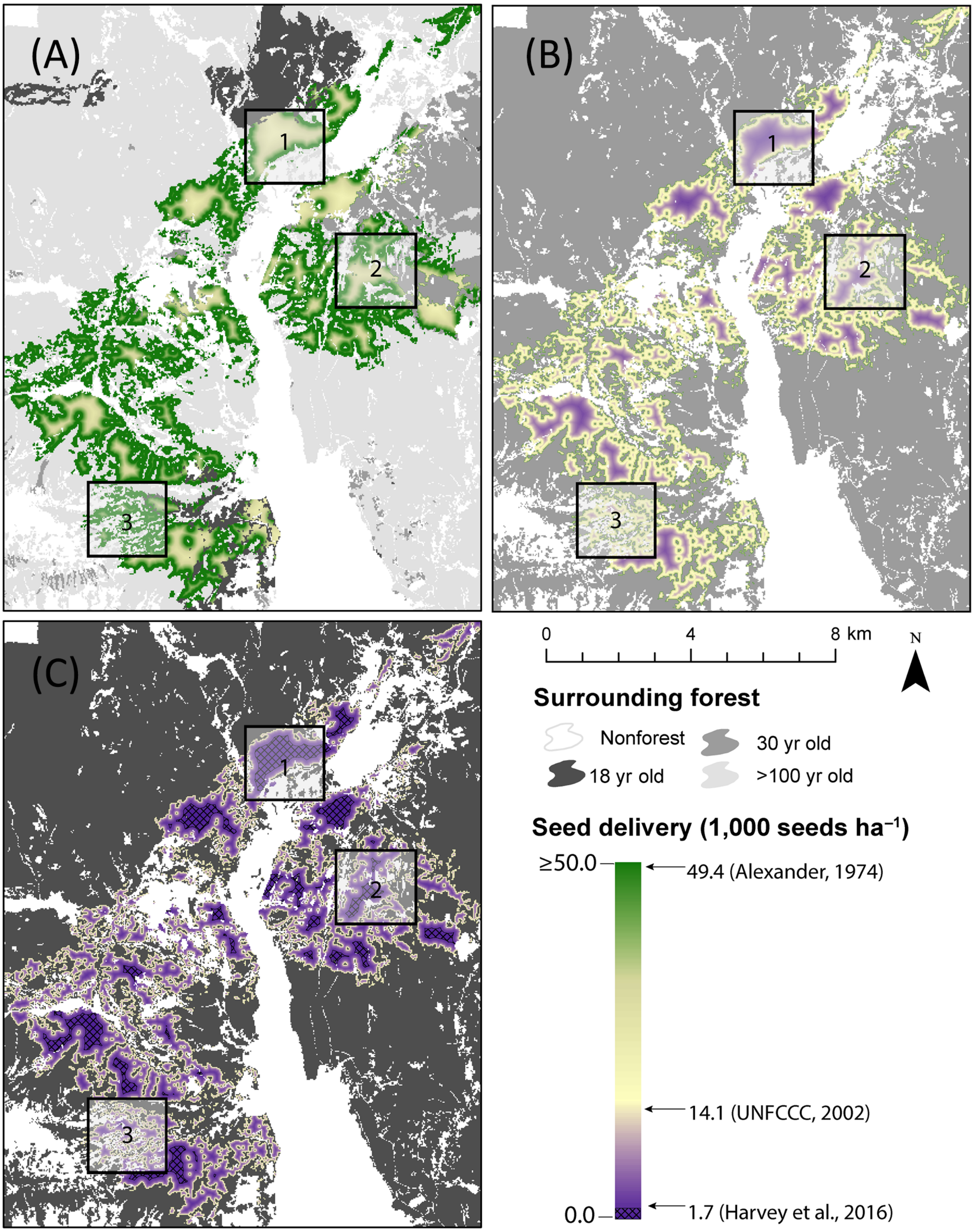

FIG. 5. Estimated *Pinus contorta* seed delivery under three scenarios. (A–C) represent scenarios under actual forest structure, homogeneous 30-yr-old forest, and homogeneous 18-yr-old forest, respectively. Estimated seed delivery after the 2016 Berry Fire is insufficient to meet the most stringent definition of forest cover in large burned areas, but entirely exceeds less stringent threshold definitions (A). In the 30-yr-old scenario, none of the burned area meets the highest threshold, but none falls below the most critical threshold, either (B). Large patches in the 18-yr-old scenario fall below even the most critical threshold, and nowhere is the highest threshold met. Detailed maps of the areas in Boxes 1, 2, and 3 are given in Appendix S1: Fig. S3.

TABLE 2. Area meeting minimum thresholds of tree density for retained forest cover according to three definitions.

Scenario	Area meeting threshold definition (ha; % of study area): 1,480 stems/ha	424 stems/ha	50 stems/ha	Seed delivery (seeds/m^2) 600 m from edge
2016 Berry Fire	2,360 ha; 54%	4,340 ha; 100%	4,340 ha; 100%	2.1
All 30-yr edges	0 ha; 0%	3,040 ha; 70%	4,340 ha; 100%	0.3
All 18-yr edges	0 ha; 0%	1,000 ha; 23%	3,830 ha; 88%	<0.1

Notes: Definitions of minimum *Pinus contorta* tree density for forest cover are referenced in Appendix S1: Table S3. In addition to the estimated single-year seed delivery following the Berry Fire, annual seed delivery was estimated for scenarios in which surrounding forest was entirely 30 yr old and 18 yr old.

Under the scenario in which the entire live edge was 18 yr old, projected annual *P. contorta* seed delivery averaged 9,000 seeds/ha and varied from 0 to 23,500 seeds/ha (an estimated reduction of 83.44%). None of the severely burned areas in this scenario met the 49,400 annual seeds/ha threshold. Twenty-three percent of the study area met the moderate threshold of 14,100 seeds/ha. Twelve percent (521 ha) of the burned area was expected to receive insufficient seed to meet the critical threshold of 1,700 seeds/ha in this scenario (Table 2, Fig. 5C; Appendix S1: Fig. S3C).

DISCUSSION

Results of this study indicate that seed dispersal is substantially reduced in postfire subalpine forests when the surrounding live forest is also young. Not only is seed supply low (immaturity risk; Keeley et al. 1999), but seeds do not travel far from the short-statured young trees at edges of reburned forest. Thus, effects of short-interval fire on tree regeneration may compound in ways that undermine both serotiny (in situ dispersal) and wind dispersal (ex situ dispersal)—the principle mechanisms by which seed is delivered to subalpine forests after high-severity fire (Johnstone et al. 2016). Proximity to seed sources plays a particularly important role for regeneration of obligate seeders (i.e., no ability to resprout) following fire when a canopy seedbank is lacking (Tautenhahn et al. 2016, Hansen et al. 2018). Changes in these key processes could compromise the resilience of historically fire-adapted forests to increasing fire activity. Because the Berry Fire burned forests of varying age, there appears to be sufficient older live forest in this study area to ensure seed delivery within the burn perimeter. However, our forest-age scenarios demonstrated that seed dispersal into high-severity burns will be very limited if surrounding forests are dominated by immature and short-statured trees. Dispersal kernels that do not account for the height of surrounding forest may overestimate seed dispersal into burned forests as fire intervals decrease and young forests increasingly burn. As a result, postfire tree establishment could presently be overestimated following short-interval fire (Airey Lauvaux et al. 2016, Harvey et al. 2016, Rother and Veblen 2016), adding uncertainty to projections of forest recovery.

The range of values in propagule pressure we observed were consistent with other studies of *P. contorta* (Lotan and Critchfield 1990). Estimates from seed traps in live forests also aligned closely with observed patterns of seed delivery in the first 5 m of burned transects. Thirty years postfire, seed sources of *P. engelmannii* and *A. lasiocarpa* were absent in stands we observed (Appendix S1: Tables S5 and S6), and propagule pressure was low compared to older stands, supporting that repeated short-interval fires may over time reduce the prominence of these nonserotinous, shade-tolerant species on the landscape and contribute to broad-scale shifts in species composition (Schoennagel et al. 2004, Enright et al. 2015). However, given that sexually mature *A. lasiocarpa* and *P. engelmannii* were very sparse along live forest edges surrounding the burned area (especially when <30 yr old; Appendix S1: Table S5), it is reasonable to assume that some of the seeds collected in burned patches dispersed from trees farther away than the nearest live edge (Nathan and Muller-Landau 2000*b*). Thus, although *A. lasiocarpa* and *P. engelmannii* seed delivery was low, their true dispersal distance may be much farther than the distances we measured. Determining these true distances is beyond the scope of the current study. The seed delivery rates of these nondominant conifers were high relative to the abundance of nearby potential seed sources, suggesting that *A. lasiocarpa* and *P. engelmannii* may indeed disperse farther than *P. contorta* (Shearer 1986), despite our finding that realized *P. contorta* seed densities within these burned patches was much higher.

Counter to our expectations, the magnitude of *P. contorta* propagule pressure within and seed delivery from 30-yr-old stands and edges was substantial. *Pinus contorta* do in fact produce cones within one to two decades, with nonserotinous cones dominating the cone bank for several decades (Lotan 1976, Turner et al. 2007, 2016). Within 30 yr postfire, *P. contorta* stands may produce sufficient seed to maintain resilience near live-forest edges, even if fire-return intervals fall below 50 yr (which is expected; Westerling et al. 2011, Liu et al. 2013). However, although 30-yr-old stands may release abundant seed from nonserotinous cones, their total seedbank is much smaller than older stands (Muir and Lotan 1985, Turner et al. 2016). And although seed delivery within the live 30-yr-old and >100-yr-old *P. contorta* stands was similar, seed-dispersal distances along burned transects were much greater from the older, taller live trees.

Tree height, which is correlated with tree age, was a primary driver of seed-dispersal distance into burned areas. For wind-dispersed seeds, release from a higher position in the canopy should lead to farther dispersal distances (Greene and Johnson 1989, 1996). Thus, dispersal from tall live edges is an important mechanism for postfire tree regeneration across large burned patches (hundreds of meters). Shorter intervals between fires can prevent sufficient supply of in situ seed from serotinous cones by reducing the time available for seedbank production and by completely consuming cones when they are on young trees near the ground (Keeley et al. 1999, Brown and Johnstone 2012, Enright et al. 2015, Johnstone et al. 2016, Turner et al. 2019). Thus, dispersal from nonserotinous live trees will be increasingly important under future climate. However, as fire size and frequency increase, a higher proportion of the landscape will be dominated by younger, shorter-statured forest and distances from old, tall-statured seed sources will increase.

Among potential predictors explored in this study, several were surprisingly unimportant. For example, we found no directional effect of wind on seed delivery. This may have been because winds tended to switch to the opposite direction diurnally, and/or because the direction of wind gusts was not always consistent with prevailing wind direction (Appendix S1: Fig. S4). The temporal resolution of our seed collection would have captured only a net effect of wind on seed delivery throughout the season. Although we did find a statistically significant effect of the density of fire-killed trees (snags) on seed delivery in burned forest, snag density was strongly correlated with tree height ($r = -0.61$). We did not include snag density in our final dispersal kernel model because tree height was a stronger independent predictor. This suggests that if snags either impeded or enhanced seed dispersal, as might be expected from foliated live trees and canopies (Nathan et al. 2002, Damschen et al. 2014), the effect was weak relative to the influence of seed release height. Cone abundance per se was also not identified as a strong predictor, possibly because, counter to our expectations, edges of varying age yielded similar numbers of cones because of a trade-off in cones per tree and stem density (Appendix S1: Fig. S2). Alternatively, the low importance of this variable may be explained in part by limitations of our data collection. Nonserotinous *P. contorta* cones take 2 yr to mature, and we did not distinguish between mature and immature cones in our cone abundance observations; similarly, we did not quantify serotinous and nonserotinous cones separately when both were present on a single tree. Only mature nonserotinous cones can supply seed for dispersal without the high temperatures of fire. Despite these limitations, tree height is tightly correlated with tree age (and thus with cone supply as well). Therefore, tree height may characterize cone abundance in addition to seed release height.

Although distant stands of >100-yr-old forest can deliver seed across large burned areas, even small burned patches may become insurmountably wide when young forests reburn and surrounding live forests are dominated by <30-yr-old trees. Dominance of young, short-statured trees surrounding burned areas effectively compresses the dispersal kernel in space, meaning the difference between seed delivery from young and old live-forest edges is most pronounced at greatest distances into burned areas. Islands of surviving legacy trees within the perimeter of stand-replacing fires can promote ecosystem recovery by providing a seed source for post-fire regeneration (Keeton and Franklin 2005). Stands that repeatedly serve this role over multiple fires (i.e., fire refugia) can be an important component of forest resilience (Turner et al. 1998, Kemp et al. 2016, Meddens et al. 2018).

Seed supply is necessary, but alone, is insufficient for forest regeneration. Many other factors (e.g., seed predation, germination rate, survivorship, and establishment success) will also determine whether a forest regenerates (Nathan and Muller-Landau 2000*b*, Davis et al. 2018). Our estimates of the quantity of seed delivery necessary for forest recovery assumed for simplicity a constant (and generous—see Lotan and Perry 1983, Koch 1996) ratio of seeds to established trees. However, a warmer, drier future climate may reduce germination and early survival of *P. contorta* and other conifers native to the Greater Yellowstone Ecosystem (GYE; Andrus et al. 2018, Davis et al. 2019, Hansen and Turner 2019), further exacerbating consequences of immaturity risk and short-distance seed dispersal. Furthermore, reductions in coarse woody debris resulting from increased fire severity (Turner et al. 2019) may increase temperatures, potentially affecting germination success. Reduced resilience of conifer species may create opportunities for deciduous species, such as *P. tremuloides* (Kulakowski et al. 2013, Tautenhahn et al. 2016, Hansen et al. 2016, Gill et al. 2017*b*), to expand on the landscape. Will burned forest surrounded by young trees regenerate over many generations? Or will windows of opportunity close as patch centers are colonized by other plants? The latter may be likely, given that postfire conditions under modern climate tend to be warmer now than they have been historically (Hansen et al. 2016, Hansen and Turner 2019). Temperatures in the GYE have already warmed (Hansen et al. 2016, Notaro et al. 2019), and future warming may lead not only to increased fire frequencies, but also altered conditions for conifer establishment and survival.

Conclusions

Our data suggest that consequences of immaturity risk are amplified when surrounding live forests are also young. As fire frequency increases in subalpine forests, the combined effect of lost in situ seed sources (e.g., serotiny) and reduced seed delivery from outside burned patches will deliver a double blow to forest regeneration after short interval fires. Because most establishment occurs soon after fire when exposed mineral soil provides an ideal seedbed (Alexander 1974, Turner et al. 1999, Johnstone et al. 2004—but see also Gill et al. 2017*a*), the temporal mismatch between seed supply and suitable conditions for germination and establishment may have long-term consequences for stand development. These compound effects are likely to become more pronounced as climate continues to warm and fire activity continues to increase (Westerling et al. 2011, Turner et al. 2019). Our results elucidate an underappreciated mechanism by which more frequent high-severity fire can catalyze substantial changes in the extent, composition, and structure of northern conifer forests.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3194/suppinfo

Data Availability

Data are available from the EDI Data Portal https://doi.org/10.6073/pasta/e193fdedace0e1af4e0b7388105329e0 (Gill et al. 2020).