



High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches

Brian J. Harvey^{1*}, Daniel C. Donato² and Monica G. Turner¹

¹Department of Zoology, University of Wisconsin, Madison, WI 53706, USA,

²Washington State Department of Natural Resources, Olympia, WA 98504, USA

ABSTRACT

Aim Climate warming and increased wildfire activity are hypothesized to catalyse biogeographical shifts, reducing the resilience of fire-prone forests world-wide. Two key mechanisms underpinning hypotheses are: (1) reduced seed availability in large stand-replacing burn patches, and (2) reduced seedling establishment/survival after post-fire drought. We tested for regional evidence consistent with these mechanisms in an extensive fire-prone forest biome by assessing post-fire tree seedling establishment, a key indicator of forest resilience.

Location Subalpine forests, US Rocky Mountains.

Methods We analysed post-fire tree seedling establishment from 184 field plots where stand-replacing forest fires were followed by varying post-fire climate conditions. Generalized linear mixed models tested how establishment rates varied with post-fire drought severity and distance to seed source (among other relevant factors) for tree species with contrasting post-fire regeneration adaptations.

Results Total post-fire tree seedling establishment (all species combined) declined sharply with greater post-fire drought severity and with greater distance to seed sources (i.e. the interior of burn patches). Effects varied among key species groups. For conifers that dominate present-day subalpine forests (*Picea engelmannii*, *Abies lasiocarpa*), post-fire seedling establishment declined sharply with both factors. One exception was serotinous *Pinus contorta*, which did not vary with either factor. For montane species expected to move upslope under future climate change (*Larix occidentalis*, *Pseudotsuga menziesii*, *Populus tremuloides*) and upper treeline species (*Pinus albicaulis*), establishment was unrelated to either factor. Greater post-fire tree seedling establishment on cooler/wetter aspects suggested local topographic refugia during post-fire droughts.

Main conclusions If future drought and wildfire patterns manifest as expected, post-fire tree seedling establishment of species that currently characterize subalpine forests could be substantially reduced. Compensatory increases from lower montane and upper treeline species may partially offset these reductions, but our data suggest important near- to mid-term shifts in the composition and structure of high-elevation forests under continued climate warming and increased wildfire activity.

Keywords

Climate change, conifer seedlings, forest resilience, Glacier National Park, Greater Yellowstone Ecosystem, Pinaceae, Rocky Mountains, succession, wildfire.

*Correspondence: Brian J. Harvey, Department of Geography, University of Colorado, Boulder, CO 80309, USA. E-mail: brian.harvey@colorado.edu

INTRODUCTION

Tree species in many high-elevation (i.e. subalpine) and high-latitude (i.e. boreal) forest ecosystems are adapted to severe, or stand-replacing, fires wherein nearly all pre-fire trees are killed by fire (Johnstone *et al.*, 2004, 2010a; Schoenagel *et al.*, 2004; Baker, 2009). In such systems, post-fire resilience (the capacity to tolerate fire without shifting to an alternative ecosystem state; adopted from Walker *et al.*, 2004) depends on successful and abundant early post-fire tree seedling establishment that drives forest structure (Kashian *et al.*, 2005) and function (Kashian *et al.*, 2006) for centuries. Climate change has a serious potential to compromise post-fire forest resilience by altering fire activity (Westerling *et al.*, 2006) and/or increasing drought stress on post-fire tree seedlings (Johnstone *et al.*, 2010b; Williams *et al.*, 2012). Stand-replacing fires may accelerate climate-induced biogeographical shifts already occurring in the absence of fire (Bell *et al.*, 2014a; Dobrowski *et al.*, 2015) and high-elevation forests are particularly vulnerable (Bell *et al.*, 2014b). Concerns are particularly heightened in temperate (Millar & Stephenson, 2015) and boreal forests (Gauthier *et al.*, 2015) world-wide. In such systems, robust empirical field data from actual wildfires are needed to test whether shifts in post-fire regeneration are already occurring, and anticipate when, where and why transitions might be expected to continue in the future (Trumbore *et al.*, 2015).

Two key mechanisms governing post-fire regeneration in forests with stand-replacing fire regimes are seed delivery and seedling establishment in recently burned areas. Assuming sufficient seed supply, seed delivery into stand-replacing patches depends on patch size (which determines distances from surviving trees; e.g., Turner *et al.*, 1994; Donato *et al.*, 2009) and seed-dispersal traits of dominant trees. Potential dispersal distances for many conifer species are known (e.g., Greene *et al.*, 1999), but how actual post-fire establishment of tree seedlings varies with distance to the edge of stand-replacing patches has received less attention (but see for examples Donato *et al.*, 2009; Kemp *et al.*, 2016) and may vary among species if future burn-patch sizes increase. Once seeds arrive in a stand-replacing burned patch, successful germination and seedling establishment are governed by climate conditions and local site factors (e.g. topographic setting, competition). Drought stress is a leading cause of tree mortality (Williams *et al.*, 2012), and early post-fire conifer seedlings are particularly vulnerable to prolonged drought. Subalpine and boreal forests demonstrate enormous capacity for resilience when large, severe fires are followed by suitable climate conditions [e.g. the 1988 Yellowstone fires (Turner *et al.*, 1997; Romme *et al.*, 2011) or 20th-century boreal forest fires (Johnstone *et al.*, 2004)], but consequences for tree regeneration when large fires are followed by drought are less clear. Until recently there have been limited opportunities to test coupled effects of post-fire drought and distance to seed source on post-fire tree seedling establishment across multiple burned landscapes.

Subalpine forests of the Northern Rocky Mountains in the United States provide a natural laboratory to test hypotheses about how climate warming and associated increases in fire size may affect forest resilience. Since the mid-1980s, the region has experienced disproportionate increases in wildfire activity relative to other western US areas (Westerling *et al.*, 2006; Morgan *et al.*, 2008), and post-fire climate conditions following recent large fire years have varied substantially (Westerling *et al.*, 2011). Since 1984 over a million hectares of forest (c. 5% of the total forested area of the US Northern Rockies) have burned in stand-replacing fire (Harvey, 2015), and most area is designated as wilderness, so post-fire patterns of tree seedling establishment are largely not confounded by post-fire management or recent intensive land use. Further, this large region shares many tree genera and species with subalpine and boreal forest biomes world-wide, allowing broad inference to extensive forested regions.

Variability among species in fire-related regenerative strategies (broadly applicable traits generalizable across regions; Agee, 1993; Baker, 2009) (Table 1) may drive contrasting responses to distances to post-fire seed sources and post-fire drought (thus catalysing biogeographical shifts), but net effects on overall regeneration are not known. The regenerative strategies of conifer trees range from fire 'invaders' that seed in from adjacent unburned trees and may respond negatively to increasing burn patch size, to 'avoiders' that are fire sensitive (as well as shade tolerant) and attain their greatest relative dominance in late seral conditions, to 'evaders' and 'endurers' that persist within burned patches via on-site seed sources or resprouts, respectively (Table 1). Subalpine forests contain more fire avoiders, evaders and medium- to heavy-seeded invaders, while montane forests (slightly lower in elevation than subalpine forests, and generally expected to move upslope as the climate warms) contain more light-seeded invaders, endurers (i.e. resprouters) and resisters that survive fire via thick bark (Table 1).

In this study, we quantified post-fire tree seedling establishment in stand-replacing patches of 11 different fires that occurred between 1994 and 2003 across the Northern Rocky Mountains to examine the temporal and spatial patterns of regeneration under varying post-fire climate conditions. We tested for evidence consistent with the hypothesis that future climate warming and wildfire activity will alter forest resilience. Specifically, we asked: (1) How does post-fire tree seedling establishment in stand-replacing patches vary with two key factors expected to increase with changing climate: drought severity during the initial post-fire years and distance to post-fire seed source? (2) How does the strength of the relationship between seedling establishment and these factors vary among tree species with different fire-related traits or in different biogeographical (i.e. elevational) zones? We also tested how post-fire tree seedling establishment varies with other local factors (e.g., biotic interactions). We expected post-fire tree seedling establishment to decrease for all species with increasing post-fire drought severity, but most strongly for present-day subalpine species that establish

Table 1 Fire regeneration strategy and fire related traits for common tree species in upper montane and subalpine forests of the US Northern Rockies.

Scientific name	Common name	Fire-regeneration strategy ¹	Important fire-related traits ^{2,3}			
			Bark thickness	Seed dispersal	Seed weight	Shade tolerance
<i>Pinus contorta</i>	Lodgepole pine (serotinous)*	Evader	Thin	Aerial seedbank	Medium	Very low
<i>Pinus contorta</i>	Lodgepole pine (non-serotinous)*	Invader	Thin	Wind	Medium	Very low
<i>Picea engelmannii</i>	Engelmann spruce*	Avoider	Thin	Wind	Medium	Moderate
<i>Abies lasiocarpa</i>	Subalpine fir*	Avoider	Thin	Wind	Heavy	Very high
<i>Pseudotsuga menziesii</i>	Douglas-fir†	Resister/invader	Thick	Wind	Medium	Moderate
<i>Larix Occidentalis</i>	Western larch†	Resister/invader	Thick	Wind	Light	Very low
<i>Populus tremuloides</i>	Quaking aspen†	Endurer/invader	Thin	Resprouting/wind	Very light	Low
<i>Pinus albicaulis</i>	Whitebark pine*‡	Invader	Thin	Animal	Very heavy	Moderate

¹Agee (1993); ²Baker (2009); ³Minore (1979).

*Tree species is currently most abundant in the subalpine forest zone.

†Tree species is currently most abundant in the montane forest zone.

‡Tree species is currently most abundant at the upper treeline forest zone.

early after fire (and are therefore more vulnerable to post-fire drought). We expected post-fire tree seedling establishment to decrease toward the interior of stand-replacing patches for fire avoiders, resisters and invaders, but not for fire evaders or endurers that can retain on-site propagules. We expected upper montane species to exhibit dampened (or no) responses to post-fire drought, indicating potential upward shifts in their elevational extent as subalpine forests potentially contract.

METHODS

Study area

We studied two focal regions in the Northern Rocky Mountains of the United States – Glacier National Park (hereafter ‘Glacier’) (48°46' N, 114°00' W) and the Greater Yellowstone ecosystem (hereafter, ‘Greater Yellowstone’) (44°10' N, 110°15' W), which together comprise over 75,000 km² of mountainous conifer forest. Most land is federally protected and managed as wilderness (Glacier, Yellowstone and Grand Teton National Parks; and portions of surrounding national forests). The climate in both regions consists of cool summers (c. 20 °C average daily July temperature) and cold winters (−15 °C average daily January temperature), with most precipitation falling as winter snow and spring rain. Greater Yellowstone is warmer and drier than Glacier, resulting in a 21% greater water-year cumulative moisture deficit from 1983 to 2012 in our Greater Yellowstone study fires (source Westerling *et al.*, 2011).

Subalpine forests occupy mountain slopes and plateaus from c. 1000–2000 m elevation in Glacier and from c. 2000–3000 m elevation in Greater Yellowstone; lower elevations in Glacier are a result of the c. 4.5° increase in latitude compared with Greater Yellowstone (Fig. 1). Forests are largely dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta* var. *latifolia*), and correspond to the *Abies lasiocarpa* Series as described by Arno (1980). These species have relatively thin

bark and are easily killed by fire, but can rapidly colonize burned areas from seed within a few years of fire. Lodgepole pine can produce seed in non-serotinous cones that rely on wind dispersal or serotinous cones that require heat for seed release; the level of serotiny typically decreases with increasing elevation and fire-return interval (Tinker *et al.*, 1994; Schoennagel *et al.*, 2003). Montane forests at lower elevations include western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and occasional stands of quaking aspen (*Populus tremuloides*). Upper treeline forests at higher elevations include bird-dispersed whitebark pine (*Pinus albicaulis*). Fire regimes in subalpine forest are characterized by infrequent (150–300-year interval) stand-replacing wildfires that are primarily driven by prolonged periods of warm, dry and windy conditions (Arno, 1980; Romme & Despain, 1989; Barrett *et al.*, 1991; Barrett, 1994; Kipfmüller & Baker, 2000; Schoennagel *et al.*, 2004) and are often followed by generally abundant post-fire tree regeneration (e.g. Romme *et al.*, 2011).

We sampled stands in pre-fire mature forests (i.e. with no evidence of recent pre-fire disturbance) with mean pre-fire basal area of 35 ± 1 m² ha^{−1} (±SD) and a stand density of 443 ± 14 large (≥15 cm d.b.h.) trees ha^{−1}. Pre-fire stands were primarily dominated by subalpine fir, Engelmann spruce and lodgepole pine (Table 2). Western larch was present pre-fire in nearly half of the Glacier stands (but does not occur in Greater Yellowstone), and stands had minor pre-fire components of Douglas-fir and whitebark pine in Glacier and Greater Yellowstone, respectively.

Study design

Plots in each study area were located in patches of stand-replacing fire in wildfires that burned in 1994, 1999, 2000, or 2003 (Fig. 1). These years represent widespread fire years in the US Northern Rockies (Morgan *et al.*, 2014), and they cover a wide range of regional and local post-fire climate conditions. For each fire, we identified candidate stand-

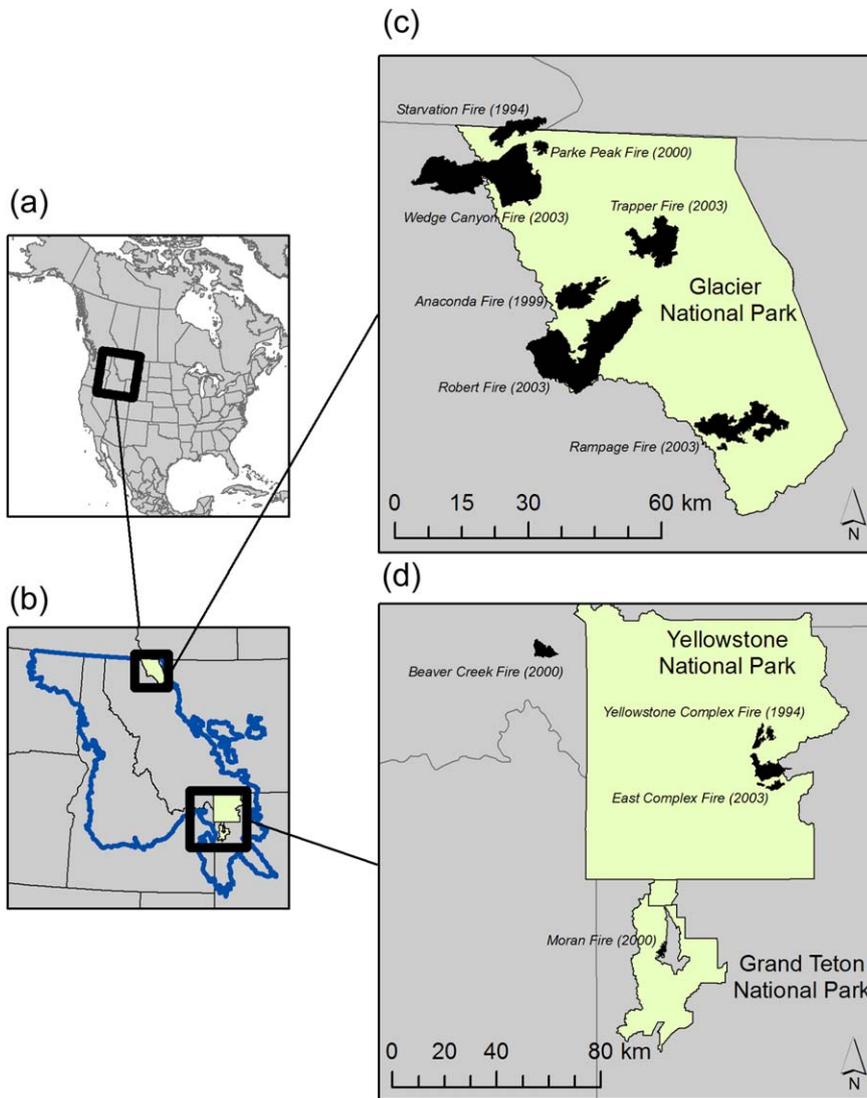


Figure 1 Study area map. (a) Location of US Northern Rockies in North America. (b) Location of each study area within the US Northern Rockies Ecoregion (outlined in blue). (c) The Glacier study area with Glacier National Park (NP) highlighted in green and each study fire shaded in black. (d) The Greater Yellowstone study area with Yellowstone NP and Grand Teton NP highlighted in green and each study fire shaded in black. Years of fire occurrence are in parentheses in (c) and (d).

replacing fire patches ≥ 4 ha in size that contained pre-fire subalpine forest as indicated on National Park Service vegetation maps. Patches were delineated using satellite-derived maps of burn severity (Harvey, 2015) and high-resolution aerial photographs provided by the National Park Service. Stand-replacing patches were defined as areas with $>90\%$ canopy tree mortality from fire (although mortality was most often 100%) and patch edges were defined by areas where $>25\%$ of the pre-fire canopy trees survived the fire (although survival of canopy trees was most often $>75\%$), similar to thresholds applied by Donato *et al.* (2009). From random starting points (to account for varying wind directions) along the perimeter of each stand-replacing patch, plots were situated along transects that started at the edge and continued into the interior at an angle perpendicular to the patch edge. Plots were located at progressively greater distances from the edge of the stand-replacing burn patch, at 15, 45, 90, 150, 350, 550, 750 and 1000 m, depending on patch size (one patch in Greater Yellowstone was large enough to fit a plot at 1250 m from the edge; no patches in

Glacier were large enough to fit plot distances >750 m from the edge). For each transect, we also included one control (unburned) plot 15 m away from the edge of the stand-replacing patch and aligned with the transect azimuth. Multiple transects within one fire were separated by >350 m and oriented at perpendicular angles. In total, we sampled 78 post-fire plots (14 transects, seven fires) and 14 control plots in Glacier, and 106 post-fire plots (18 transects, four fires) and 18 control plots in Greater Yellowstone. The number of transects per fire varied based on the area available for sampling within each fire. None of the sample plots contained any evidence of pre- or post-fire logging (e.g. no cut stumps) and we confirmed with regional forest managers that there was no recent pre-fire or post-fire management (e.g. tree planting or erosion control) that would have affected post-fire tree regeneration.

Field data collection

Each plot was a 30-m diameter circle (707 m²) in which we collected data on post-fire tree seedling establishment, pre-

Table 2 Topographic setting and pre-fire stand structure of the stand-replacing burn patch plots in Glacier and Greater Yellowstone.

Variable	Glacier (<i>n</i> = 78)				Greater Yellowstone (<i>n</i> = 106)			
	Min.–max.	Median	Mean (SE)	Frequency (%)	Min.–max.	Median	Mean (SE)	Frequency (%)
Topographic conditions								
Elevation (m)	1119–1847	1246	1350 (26)		2065–2687	2503	2407 (20)	
Slope (deg.)	0–24	6	7 (1)		0–47	5	7 (1)	
TMI (0–2)	0–2.0	0.9	0.9 (0.1)		0–2.0	0.3	0.7 (0.1)	
Pre-fire stand structure								
Basal area (m ² ha ⁻¹)*	18–62	31	33 (1)		16–50	36	36 (1)	
Tree density (≥ 15 cm, stems ha ⁻¹)†	142–1075	403	472 (25)		14–962	403	422 (15)	
Percentage of stems ≥ 15 cm†								
Lodgepole pine	0–38	4	7 (1)	60	0–100	19	30 (3)	75
Subalpine fir	0–92	23	28 (2)	90	0–100	39	40 (3)	90
Engelmann spruce	8–100	42	42 (2)	99	0–96	14	20 (2)	77
Western larch	0–40	0	4 (1)	44	0–0	0	0 (0)	0
Douglas-fir	0–53	3	8 (1)	55	0–38	0	1 (0)	8
Whitebark pine	0–0	0	0 (0)	0	0–90	0	5 (1)	29
Unknown	0–68	3	11 (2)	n.a.	0–45	0	4 (1)	n.a.
Pre-fire lodgepole pine serotiny (% of trees)	25–100	100	86 (11)	n.a.	0–50	0	15 (5)	n.a.

*Basal area was measured in the control (unburned) plots outside the stand-replacing burn patches.

†Tree stems (≥ 15 cm) were recorded in each post-fire plot, and included stems that had fallen since fire.

TMI, topographic moisture index [2 being wet aspects (north-east facing) and 0 being the dry aspects (south-west facing)] (Beers *et al.*, 1966); SE, standard error; n.a., not applicable.

fire stand structure, post-fire ground cover and physical site characteristics. We recorded every tree seedling established post-fire in variable-sized subplots according to the post-fire density of tree seedlings. The default subplot size was four 2 m × 15 m rectangular plots (120 m² total area) configured in cardinal directions. Subplot size was objectively decreased to four 0.5 m × 15 m belt plots (30 m² total area) or increased to the entire plot (707 m² total area) if >200 or <10 tree seedling were to be captured in the default subplot size, respectively. For each tree seedling stem in the subplots, we recorded species, height (cm), approximate age (in years, by counting the number of bud scars on the main stem and adjusting by +0.8 year; Urza & Sibold, 2013) and any evidence of animal browsing or mechanical damage.

To characterize pre-fire stand structure, we recorded standing or down (but standing pre-fire) pre-fire trees (>15 cm d.b.h.) for each species that were rooted in the plot. If pre-fire lodgepole pine trees were present we noted any evidence of serotinous cones (e.g. partially closed or highly reflexed cones on burned and/or fallen pre-fire logs; Tinker *et al.*, 1994). Distance to the nearest live, pre-fire, seed-bearing tree was measured from the centre of the plot with a TruePulse laser rangefinder. Post-fire ground cover (percentage cover of wood, litter, bryophytes, soil and rock to the nearest 5%) and post-fire vegetation cover (percentage cover of forbs, graminoids, shrubs and trees to the nearest 5%) were recorded in eight 0.25-m circle subplots. We recorded plot coordinates (UTM NAD83 Zone 12N), elevation (m), slope (degrees) and aspect (compass azimuth) from the centre of the plot.

For each control (unburned edge) plot, we measured stand basal area (m² ha⁻¹) per species using a basal area prism

(basal area factor 2) from the centre of the plot, and recorded the presence of cones on mature trees. If lodgepole pine was present, we scored each plot for percentage serotiny based on up to 12 trees nearest the centre of the plot following established methods (Tinker *et al.*, 1994). Field sampling was conducted from June to August 2013.

Post-fire drought severity

We characterized drought severity during the first four post-fire years (years 0–3 post-fire) because severe drought could potentially reduce tree seedling establishment during a window of time that is often characterized by a pulse of establishment when seedbed conditions are ideal and competition with shrubs and herbs is limited. Monthly climate data for the period 1983–2012 were extracted for each plot from an existing 12 km × 12 km gridded dataset (Westerling *et al.*, 2011). To characterize early post-fire drought severity, we used average water-year (October to September) cumulative moisture deficit (mm) for years 0–3 post-fire. To account for among-site variation in climate settings, we standardized drought severity for each plot by rescaling cumulative moisture deficit values for the 3-year post-fire time window to ± SD of the local 1983–2012 average. Thus, our post-fire drought severity index was relative to each location.

Statistical analyses

The number of post-fire tree seedlings for each species that established each year (based on bud scars) in each plot was standardized to seedlings ha⁻¹ by dividing the total number of seedlings (dated to each year of establishment) by the plot

sample area. We qualitatively characterized temporal patterns of seedling establishment for each species by plotting the annual number of seedlings established ha^{-1} in each post-fire year, averaged across all plots within in each region (Glacier and Greater Yellowstone). Because of moderate confidence in estimating the ages of conifer tree seedlings from bud-scar counts in the absence of destructive sampling (which was not permitted in our study area), temporal trends of seedling establishment were not included in any quantitative analyses. Instead, temporal trends are included to aid in the interpretation of our overall analysis of tree seedling establishment (which was not dependent on tree ages). Temporal trends in quaking aspen establishment were not assessed because no published relationships are available between bud scars and tree seedling age.

To test for effects of our two focal independent variables (post-fire drought severity and distance to the nearest seed source) on post-fire tree seedling establishment we used generalized linear mixed models with a log-link (family = quasi-Poisson) to account for over-dispersed count data. One model was constructed for overall tree seedling establishment (especially relevant if species complementarity allows compensatory establishment), and separate models were constructed for each tree species. The response variable for each model was the total number of seedlings present at the time of sampling, divided by the number years since the fire; we normalized the rate of seedling establishment (seedlings ha^{-1} year $^{-1}$) to account for varying time since fire in our study design. The unit of analysis was the plot, which was the level at which each variable was measured. We included a random-effects term for each transect to account for grouping of plots along transects. The total sample size for models included all plots ($n = 184$), except for lodgepole pine which was separated into two models: one for plots containing pre-fire serotiny ($n = 59$) and one for plots where pre-fire serotiny was absent ($n = 125$).

All models initially included a suite of variables that potentially affect post-fire tree seedling density, generally falling into categories of climate, fire and local factors (Table 3). Each saturated model (including all terms at the start) was then iteratively trimmed until only significant ($P \leq 0.05$) terms remained. Final models were assessed for fit by plotting and calculating the squared difference between fitted versus observed values. As a measure of model fit, this number is reported as a 'pseudo- R^2 ', as true model R^2 values for generalized linear mixed models are not available. Although pseudo- R^2 calculations for generalized linear mixed models have been proposed (Nakagawa & Schielzeth, 2013), there are no such calculations that we know of for models with quasi-Poisson error distributions. Therefore, although we realize our straightforward calculation of a pseudo- R^2 value is likely to overstate the explanatory power of fixed effects in our models, it provides a useful comparison of relative model fit among tree species in our study. To allow for direct comparison of effect sizes among different variables in each model, predictor-variable effect sizes were standardized (scaling to a

Table 3 Candidate predictor variables included in models of post-fire tree seedling establishment.

Factor	Variable	Description (units, data range)
Climate	Region Glacier or Greater Yellowstone	Cooler/wetter region (Glacier) – 30-year mean of 210 mm cumulative moisture deficit; warmer/drier region (Greater Yellowstone) – 30-year mean of 255 mm cumulative moisture deficit
	Post-fire drought severity	
	Cumulative moisture deficit	Water-year (October–September) cumulative moisture deficit averaged across 1, 2 and 3-years post-fire (\pm SD from the 30-year mean from 1983–2012, –1.27 to 1.11)
	Local microclimate Topographic moisture index	Cosine-transformed aspect reflecting similarity of plot aspect to north-east, which is the coolest/wettest aspect (Beers <i>et al.</i> , 1966) (index with 0.0 = south-west and 2.0 = north-east, 0.0 to 2.0)
Fire	Distance to seed source	
	Distance to pre-fire live tree	Distance from plot centre to the nearest pre-fire live seed-bearing tree (5–750 m)
	Distance to patch edge	Distance from plot centre to the nearest edge of the stand-replacing burn patch (15–1250 m)
	Burn severity RdNBR	Satellite index of burn severity for the plot, using the relative differenced normalized burn ratio (RdNBR), which detects canopy and surface fire effects (Miller & Thode, 2007) (320–1475)
Local factors	Seed supply	
	Presence pre-fire	Presence of the post-fire tree species in the plot prior to the fire (yes/no)
	Stems pre-fire	Pre-fire stems (> 15 cm d.b.h.) in the plot for the post-fire tree species (proportion of total stems, 0 to 1)
	Local topography Slope	Slope measured from plot centre (0–47°)
	Biotic interactions Shrub cover	Cover of shrubs averaged from eight 0.25-m ² subplots within each plot (proportion of total cover, 0.00–0.74)

Table 4 Post-fire tree seedling establishment normalized by time since fire (post-fire seedlings ha⁻¹ year⁻¹) in the stand-replacing burn patch plots.

Tree species	Glacier (<i>n</i> = 78)				Greater Yellowstone (<i>n</i> = 106)			
	Min.–max.	Median	Mean (SE)	Frequency (%)	Min.–max.	Median	Mean (SE)	Frequency (%)
All tree species combined	3–33,067	1055	4454 (819)	100	0–2035	45	232 (39)	96
Lodgepole pine	0–8400	170	570 (147)	74	0–1800	26	192 (34)	92
Subalpine fir	0–933	0	50 (16)	38	0–167	0	6 (2)	36
Engelmann spruce	0–27,733	251	3177 (706)	81	0–632	0	13 (7)	37
Western larch	0–4133	37	357 (83)	77	0–0	0	0 (0)	0
Douglas-fir	0–2933	6	241 (61)	41	0–6	0	0 (0)	8
Whitebark pine	0–267	0	6 (4)	5	0–176	0	8 (2)	43
Quaking aspen	0–1067	0	44 (15)	32	0–359	0	13 (4)	36

SE, standard error.

mean of zero, with each value represented as \pm SD from that variable's mean). All statistical analyses were conducted in R (R Development Core Team, 2012) using the *glmmPQL* function in the 'MASS' package (Venables & Ripley, 2002).

RESULTS

Ninety-eight per cent of plots contained post-fire tree seedlings, and establishment rates ranged from 0 to 33,067 seedlings ha⁻¹ year⁻¹. Rates of establishment of tree seedlings spanned four orders of magnitude in each region. Mean and median annual seedling establishment rates were one and two orders of magnitude higher, respectively, in Glacier than Greater Yellowstone (Table 4, Fig. 2). By 10 years after fire in Glacier, there was an average increase of 105-fold in the number of pre-fire trees to post-fire tree seedlings per plot (i.e. the number of post-fire seedlings compared with the number of pre-fire stems >15 cm d.b.h.), and post-fire seedling density exceeded pre-fire stem density in 95% (74/78) of plots. Engelmann spruce was the most abundant post-fire tree seedling, followed by lodgepole pine, western larch and Douglas-fir. In Greater Yellowstone, there was an average five-fold increase in the number of pre-fire trees to post-fire tree seedlings per plot by 10 years after fire, and post-fire seedling density exceeded pre-fire stem density in 53% (56/106) of plots. Lodgepole pine was most abundant, followed by Engelmann spruce, quaking aspen and whitebark pine. In both regions, post-fire subalpine fir establishment was relatively sparse, despite it being the most abundant pre-fire tree.

Temporal patterns of post-fire tree seedling establishment

Temporal patterns of seedling establishment varied by species. Lodgepole pine (evader/invader) establishment was characterized by a distinct pulse of seedlings 1 year post-fire, followed by protracted establishment *c.* 3–5 years post-fire (Fig. 2a, f). Establishment of avoiders (Engelmann spruce and subalpine fir) and resister/invaders (western larch and Douglas-fir) began immediately post-fire and peaked by

c. 4–6 years post-fire in Glacier (Fig. 2b–e). Establishment peaks (i.e. the year of greatest seedling establishment) for avoiders and invaders (whitebark pine) were generally later and less pronounced in Greater Yellowstone (Fig. 2g–i). Length of the establishment period across all species (the time by which 90% of seedlings were established) was 7 years, ranging from 6 years in Glacier to 12 years in Greater Yellowstone.

Post-fire drought severity and distance to post-fire seed source

Overall post-fire tree seedling establishment decreased with greater post-fire drought severity (Tables 5 & 6, Fig. 3a). Among tree species that dominated pre-fire forests, fire avoiders (Engelmann spruce and subalpine fir) decreased with more severe post-fire drought, whereas establishment of evaders (serotinous lodgepole pine) and invaders (non-serotinous lodgepole pine) was unrelated to post-fire drought severity (Tables 5 & 6, Fig. 3b). Post-fire seedling establishment for upper montane species (western larch, Douglas-fir and quaking aspen) and upper treeline species (whitebark pine) was unrelated to post-fire drought severity, regardless of their fire regeneration strategy (Tables 5 & 6, Fig. 3c). Overall post-fire tree seedling establishment decreased with greater distance to post-fire seed source, but the relationship varied among species (Tables 5 & 6, Fig. 3). Post-fire tree seedling establishment declined with increasing distance to seed source for early post-fire subalpine forest invaders (non-serotinous lodgepole pine) and fire avoiders with medium-weight to heavy seeds (Engelmann spruce and subalpine fir), but not for fire evaders (serotinous lodgepole pine). For upper montane forest and upper treeline forest species, post-fire tree seedling establishment was unrelated to the distance to seed source, regardless of the fire-related regeneration strategy.

Other factors related to post-fire seedling establishment

Other factors related to post-fire tree seedling establishment varied among species (Tables 5 & 6, Fig. 3). Post-fire seedling establishment was greater on cooler/wetter (i.e. more north-

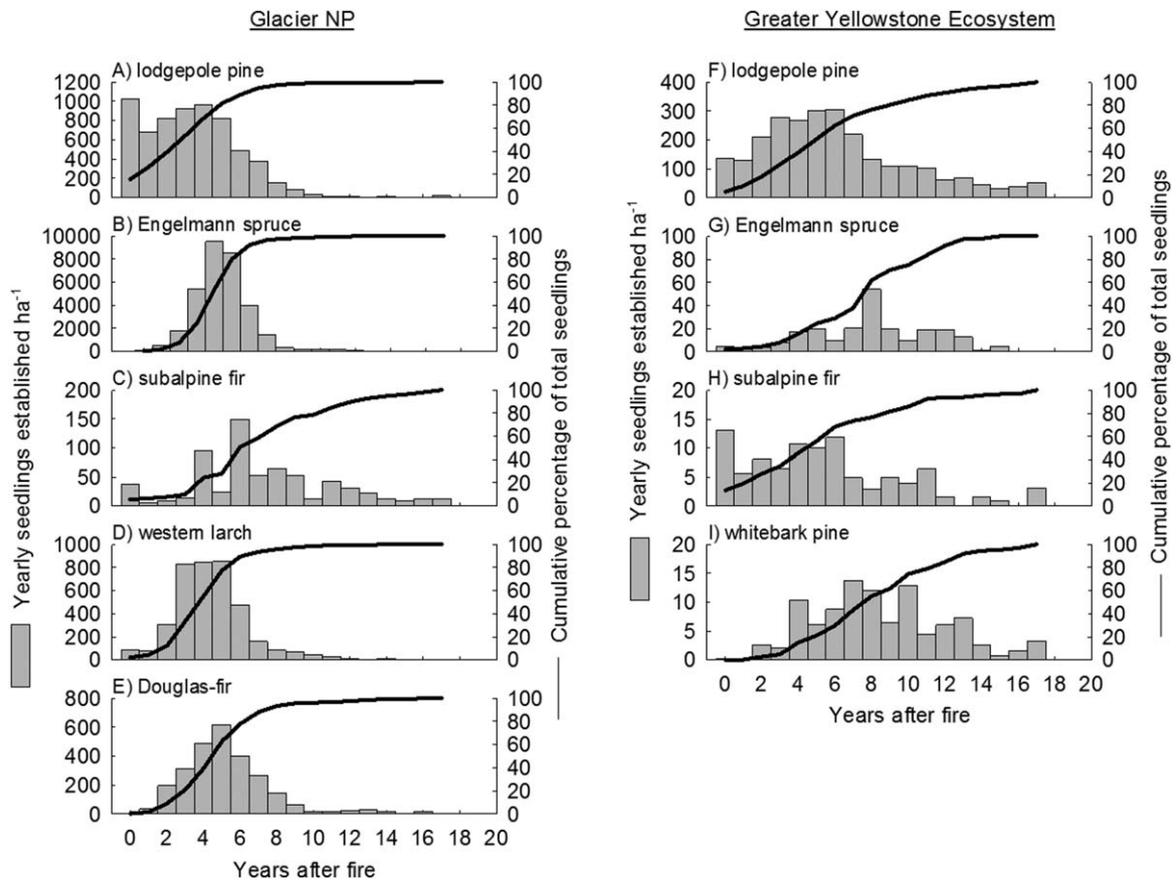


Figure 2 Temporal trends of post-fire tree seedling establishment (seedlings ha⁻¹ in each post-fire year) for each species in each study region. Data are means across all plots in each study region. Grey shaded boxes represent the number of seedlings established each year; black lines represent the cumulative percentage of all seedlings established by a given year.

easterly) aspects for all species combined (Fig. 3a), and for Engelmann spruce and whitebark pine individually (Fig. 3b, c). Overall establishment of tree seedlings was unrelated to burn severity (Tables 5 & 6, Fig. 3a), but post-fire establishment of quaking aspen increased with burn severity (Fig. 3b). For all dominant pre-fire subalpine forest species, post-fire establishment increased with local pre-fire abundance of the tree species (Fig. 3b). Slope and post-fire shrub cover were unrelated to total post-fire tree seedling establishment (Fig. 3a), but effects for both varied among tree species. Post-fire seedling establishment of serotinous lodgepole pine, western larch and Douglas-fir was greater on steeper slopes, whereas establishment of Engelmann spruce decreased on steeper slopes (Fig. 3b, c). The only species for which post-fire seedling establishment was related to post-fire shrub cover was quaking aspen, which decreased with greater shrub cover (Fig. 3c).

DISCUSSION

Our study provides empirical evidence consistent with the hypothesis that large fires followed by severe drought (both expected manifestations of climate change) influence forest resilience. The substantial decrease in subalpine species without associated increases in upper montane or upper treeline species

suggests that the net effect of climate warming and increased fire activity will likely be near- to mid-term decreases in tree densities. The mechanisms we evaluated are general to forests throughout the Northern Hemisphere that are adapted to crown fires (e.g. subalpine and boreal forests) and share similar taxa (Turner & Romme, 1994), and our results suggest important effects on the distribution and extent of such forests.

Rapid post-fire tree seedling establishment

We found relatively synchronous early post-fire establishment of fire evaders, invaders, avoiders and resisters – covering a range of shade tolerances and seed weights. These trends are characteristic of Rocky Mountain subalpine forests (Turner *et al.*, 1999; Kipfmüller & Kupfer, 2005; McKenzie & Tinker, 2012) and boreal forests in Canada (Johnstone *et al.*, 2004). More than 95% of tree seedlings across all species established within 10 years of fire, with establishment dates for most species peaking *c.* 2–4 years post-fire (coincident with the post-fire drought window we considered). Continued establishment may occur after our sampling (as has been observed in Douglas-fir forests in the Pacific Northwest United States; see Freund *et al.*, 2014), but our data support one aspect of precocious complexity in forest structure (Donato *et al.*,

Table 5 Results of generalized linear mixed models testing the effects of explanatory variables on post-fire tree seedling establishment rates (seedlings year⁻¹ ha⁻¹) for all species combined, and each species separately. Effects are standardized to compare among predictor variables.

Species	Predictor variables	β	SE	<i>t</i>	<i>P</i>
Total trees (all species)	Region (Greater Yellowstone)	-1.17	0.24	-4.85	<0.01
	Drought severity (\pm SD)	-0.62	0.22	-2.80	<0.01
	Topographic moisture index (north-east)	0.21	0.11	1.95	0.05
	Distance to seed source (m)*	-1.39	0.36	-3.84	<0.01
Lodgepole pine (serotinous)	Pre-fire trees (relative density)	0.40	0.19	2.07	0.04
	Slope (deg.)	0.63	0.13	4.68	<0.01
Lodgepole pine (non-serotinous)	Region (Greater Yellowstone)	-0.67	0.26	-2.60	0.01
	Distance to seed source (m)*	-0.56	0.13	-4.45	<0.01
	Pre-fire trees (relative density)	0.91	0.15	6.17	<0.01
Engelmann spruce	Region (Greater Yellowstone)	-2.09	0.51	-4.14	<0.01
	Drought severity (\pm SD)	-1.19	0.39	-3.07	<0.01
	Topographic moisture index (north-east)	0.38	0.07	5.59	<0.01
	Distance to seed source (m)*	-2.73	0.28	-9.68	<0.01
	Pre-fire trees (relative density)	0.78	0.11	6.90	<0.01
	Slope (deg.)	-0.42	0.07	-5.74	<0.01
Subalpine fir	Region (Greater Yellowstone)	-1.11	0.25	-4.49	<0.01
	Drought severity (\pm SD)	-0.74	0.19	-3.99	<0.01
	Distance to seed source (m)*	-2.11	0.52	-4.08	<0.01
	Pre-fire trees (relative density)	0.57	0.20	2.87	<0.01
Western larch	Slope (deg.)	0.48	0.09	5.26	<0.01
Douglas-fir	Slope (deg.)	0.62	0.08	7.29	<0.01
Quaking aspen	Region (Greater Yellowstone)	-1.07	0.34	-3.17	<0.01
	Topographic moisture index (north-east)	-0.32	0.15	-2.17	0.03
	Burn severity (RdNBR)	0.68	0.20	3.33	<0.01
	Shrub cover (prop.)	-0.67	0.18	-3.78	<0.01
Whitebark pine	Topographic moisture index (north-east)	0.42	0.16	2.55	0.01

*Distance (m) to the nearest pre-fire live seed-bearing tree.

SD, standard deviation; RdNBR, relative differenced normalized burn ratio (Miller & Thode, 2007).

All models were built by initially including all possible predictor variables (Table 3) and were iteratively trimmed by removing non-significant ($P \leq 0.05$) terms until all remaining terms were significant. Model fit was assessed using a pseudo- R^2 for each model calculated from the squared difference between the predicted and observed values, with values as follows: total trees - 0.72; serotinous lodgepole pine - 0.79, non-serotinous lodgepole pine - 0.67; Engelmann spruce - 0.91; subalpine fir - 0.38; western larch - 0.73; Douglas-fir - 0.47; quaking aspen - 0.74; and whitebark pine 0.28. The total sample size for models included each plot ($n = 184$) except for lodgepole pine, which was separated into two separate models: one for plots where pre-fire serotiny was observed ($n = 59$) and one for plots where pre-fire was absent ($n = 125$).

2012) in that early and late successional dominants (e.g. lodgepole pine and subalpine fir) are present immediately after a disturbance. The need to rely on bud scar counts to estimate the ages of tree seedlings was a limitation in our study. If permitted, destructive sampling of seedlings would have allowed for determination of the exact establishment year for every tree. Such data could support quantitative analysis of annual post-fire climate conditions and annual post-fire tree seedling establishment, potentially yielding deeper insight into climate regeneration dynamics.

Post-fire subalpine conifer establishment decreases with greater post-fire drought severity

Among the strongest and most consistent factors related to post-fire tree seedling establishment was moisture availability, supporting expectations from hypotheses that climate warm-

ing will affect forest resilience. The strength of these effects corresponded to scale, with regional effects being the strongest, followed by local post-fire drought and microclimate topography. Post-fire seedling densities sufficient for stand replacement were nearly twice as common, and median seedling densities two orders of magnitude higher, in Glacier as in Greater Yellowstone, corresponding to variability in regional moisture deficit.

The relationship between post-fire tree seedling establishment and local post-fire drought severity varied among species, generally following expectations that present-day subalpine tree species are especially at risk of seedling mortality from post-fire drought stress. The strong negative effects for Engelmann spruce and subalpine fir correspond to the relatively low drought tolerance of these species (Minore, 1979; Piñol & Sala, 2000). In contrast, lodgepole pine has high drought tolerance among subalpine trees (Minore, 1979;

Table 6 Summary of effects on post-fire tree seedling establishment, overall, and for each tree species. Effects are noted for terms with $P \leq 0.05$ in models summarized in Table 5.

Tree species	Fire-regeneration strategy ¹	Climate			Fire		Local factors		
		Region (GYE)	Post-fire drought severity	Top. moist. index	Distance to seed source	Burn severity	Pre-fire trees	Slope	Shrub cover
All species combined	All	–	–	+	–				
Lodgepole pine (serot.)*	Evader						+	+	
Lodgepole pine (non-serot.)*	Invader	–			–		+		
Engelmann spruce*	Avoider	–	–	+	–		+	–	
Subalpine fir*	Avoider	–	–		–		+		
Western larch†	Resister/invader	n.a.						+	
Douglas-fir†	Resister/invader	n.a.						+	
Quaking aspen‡	Endurer/invader	–		–		+	n.a.		–
Whitebark pine*‡	Invader	n.a.		+					

¹Agee (1993).

n/a, not applicable, term not tested in model (see Methods and Results); GYE, Greater Yellowstone.

*Tree species currently most abundant in the subalpine forest zone.

†Tree species currently most abundant in the montane forest zone.

‡Tree species currently most abundant at the upper treeline forest zone.

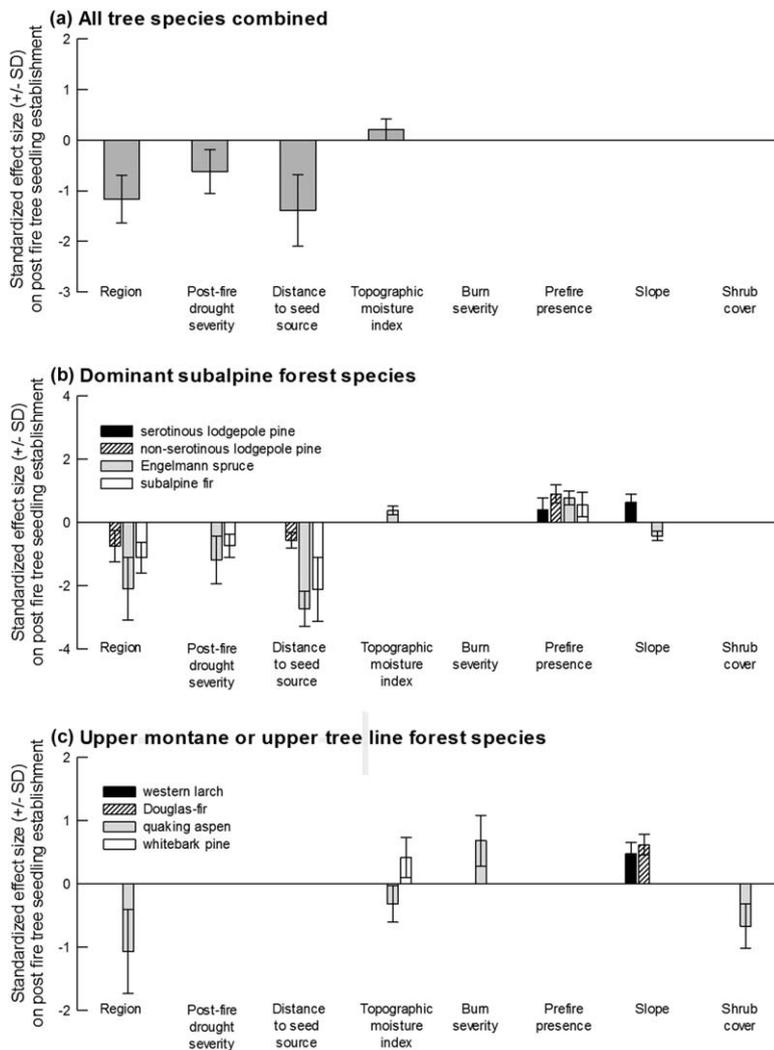


Figure 3 Modelled effects of each predictor variable on post-fire tree seedling establishment (seedlings $\text{ha}^{-1} \text{year}^{-1}$) for (a) all tree species combined, (b) dominant subalpine forest species (lodgepole pine, Engelmann spruce, subalpine fir), and (c) upper montane or upper treeline forest species (western larch, Douglas-fir, quaking aspen, whitebark pine). To allow comparison of importance among predictor variables, effects for each variable are standardized by centring on the mean and converting data points to \pm SD from the mean. Bars represent mean effect size with error bars showing 95% confidence intervals. See Table 5 for model results.

Piñol & Sala, 2000) and a capacity for extremely high post-fire seedling abundance (Turner *et al.*, 1999), providing a possible explanation for the lack of a significant relationship with post-fire drought severity. With more extreme post-fire drought, establishment of lodgepole pine seedlings may be at risk where serotiny is high because of the short regeneration window of 1–2 years post-fire (Buma *et al.*, 2013).

Post-fire seedling establishment of upper montane and upper treeline species was unrelated to post-fire drought, probably because of drought avoidance or drought tolerance. Douglas-fir is more drought tolerant than subalpine conifers (Piñol & Sala, 2000), which explains the lack of a relationship with post-fire drought severity. The dual regenerative strategies of quaking aspen (resprouting and long-distance seed dispersal) suggest that aspen might be able to use a deeper established root system to tolerate post-fire drought stress (in the case of resprouting) or possibly establish over a longer time period, allowing for drought avoidance (in the case of seeding in from outside burned patches). For whitebark pine (a fire invader), protracted post-fire seedling establishment compared with the other fire invaders (e.g. non-serotinous lodgepole pine) probably resulted in a large buffer of many years (or decades) in which some seedlings may germinate in favourable conditions. The lack of relationship between post-fire drought severity and post-fire establishment of western larch was surprising, as larch has low drought tolerance similar to subalpine trees (Minore, 1979; Piñol & Sala, 2000) and establishes quickly following fire (Fig. 2). However, larch does not occur in Greater Yellowstone (drier/warmer region), and the cooler/wetter regional climate of Glacier perhaps buffered seedlings from greater absolute post-fire drought stress. For all measures of post-fire drought we used water-year drought stress for the first three post-fire years as our measure of drought severity. It is possible that longer or shorter temporal windows of drought severity may yield additional insights into post-fire tree regeneration dynamics, but such analyses were beyond the scope of our study.

Post-fire tree seedling establishment was also related to microclimate (mediated through topographic aspect), but to a lesser degree than to regional moisture conditions or post-fire drought severity. Greater microsite moisture increases germination success (Tomback *et al.*, 2001), and our results suggest that north-east aspects may provide important local topographic refugia to buffer against severe regional post-fire drought conditions for tree species that are particularly drought sensitive. Similar findings have been reported for post-fire tree regeneration in boreal forests (Johnstone *et al.*, 2010b). Our finding that quaking aspen seedlings established at greater densities on warmer/drier (south-west) aspects may indicate that aspen can capitalize on available growing space where post-fire conifer establishment is lower.

Effect of distance to post-fire seed source varies among fire regeneration strategies

As expected, post-fire tree seedling establishment decreased with greater distances to post-fire seed source (the edge of a

stand-replacing patch or individual live pre-fire tree). Controlling for the number of plots at each distance, 75% of all post-fire tree seedlings established within 150 m of a post-fire seed source. The strength of this relationship differed among species, and was strongest for subalpine forest fire avoiders (Engelmann spruce and subalpine fir) that are easily killed by fire and possess seeds positioned high in the canopy that facilitate wind dispersal into burned areas from outside stand-replacing patches (Greene & Johnson, 1996). For lodgepole pine, the presence/absence of pre-fire serotiny dictated the importance of distance to post-fire seed source. Post-fire establishment decreased with distance to seed source in areas where pre-fire serotiny was not observed (fire invader) but not in areas with pre-fire serotiny (fire evader). These findings support patterns observed in montane forests of the US Northern Rockies (Kemp *et al.*, 2016) and in subalpine forests following the 1988 Yellowstone fires (Turner *et al.*, 1997, 2004).

For upper montane or upper treeline species, distance to post-fire seed source was unrelated to seedling establishment, regardless of fire regeneration strategy. For Douglas-fir and western larch (montane forest fire invaders with light- to medium-weight wind-dispersed seeds), the lack of significant effect could be due to the capacity for long-distance dispersal (Donato *et al.*, 2009) or an on-site seed source throughout the interior of stand-replacing patches that could have occurred from mature trees that were damaged and/or killed by fire (fire resisters) but retained a viable post-fire cone bank (Larson & Franklin, 2005). In the montane zone of the US Northern Rockies (at lower elevations than our study), post-fire Douglas-fir regeneration decreases sharply with greater distances to seed sources (Kemp *et al.*, 2016; Donato *et al.*, unpublished). Therefore, the lack of effect in our study could be from low or absent local Douglas-fir seed sources along the edge of stand-replacing patches. Quaking aspen (an upper montane endurer/invader) establishment was not related to distance to post-fire seed source, largely supporting findings in the US southern Rockies (Coop *et al.*, 2010) and in Yellowstone National Park (Turner *et al.*, 2003). Post-fire aspen seedlings have been recorded up to 15 km from seed sources (Turner *et al.*, 2003), and such a capacity for long-distance dispersal as a fire invader provides a plausible mechanism for our observed data. Heavy seeds of whitebark pine (an upper treeline fire invader) are dispersed primarily by birds (Tomback *et al.*, 2001), which often disperse seeds much farther than does wind.

Other factors of importance for post-fire tree seedling establishment

The lack of a relationship between our satellite measure of burn severity and post-fire tree seedling establishment for all species combined and for each conifer species indicates that where fires were severe enough to be effectively stand replacing, further variations in burn severity mattered little. This result was somewhat surprising, as other studies have shown that variability

between levels of stand-replacing fire (e.g. crown fire versus severe surface fire) can lead to initial differences in post-fire tree seedling establishment via different effects on canopy seed sources (Turner *et al.*, 1999; Harvey *et al.*, 2014). Our findings suggest that such effects may be lessened by more than 10 years post-fire. Alternatively, the lack of effect may also be an artefact of the modest correlation between burn severity and distance to the nearest seed source in our study ($R^2 = 0.17$), supporting findings in other studies that distance to seed source may be a proxy for (and thus subsuming explanatory power from) burn severity (Kemp *et al.*, 2016). Quaking aspen was the only species for which post-fire establishment increased with burn severity, supporting the understanding that aspen establishes well on severely burned sites (Turner *et al.*, 2003; Wan *et al.*, 2014) and may expand its current distribution with increased fire activity. Severely burned sites may provide an opportunity for aspen to invade where other trees are slower to recolonize following fire.

As expected, post-fire tree seedling establishment increased for most species with the abundance of the tree species pre-fire (a proxy for local seed source). This was not the case for upper montane forest or upper treeline forest species that were less prevalent pre-fire, and is possibly an artefact due to a limitation of our study design rather than a real biological effect. The focus of our sampling on present-day subalpine forests resulted in narrower seedling data ranges and generally lower model explanatory power (pseudo- R^2 values; see notes to Table 5) for tree species outside the subalpine forest zone pre-fire. Replicating our design along a broader elevational transect to include fires in each forest zone (lower montane, upper montane, subalpine and treeline species) may better model dynamics across the forest zones.

Our data suggest that post-fire shrub cover did not affect conifer seedling establishment, but the negative relationship between shrub cover and post-fire quaking aspen establishment suggests possible competitive or inhibitory effects from shrubs. Because pre-fire aspen stems were not observed in our plots, post-fire aspen seedlings are likely to have arrived via seed. With low shade tolerance (Burns & Honkala, 1990), aspen seedlings are probably unable to establish under dense shrub cover. Effects of slope were variable, and trends among species may have been driven by a few plots on steeper slopes rather than reflecting any biologically meaningful mechanisms. One exception would be Douglas-fir, for which greater establishment with increasing slope probably reflects a propensity to outcompete other conifers in steep terrain (Burns & Honkala, 1990).

Implications of future climate warming and wildfire activity for forest resilience

Collectively, our findings carry important implications for future forest resilience in the US Northern Rockies and similar ecosystems. By the mid-21st century, average fire seasons are expected to match or exceed the largest fire years in the historical record (Westerling *et al.*, 2011), resulting in a corresponding increase in stand-replacing patch size and distan-

ces to seed source (Harvey, 2015). Post-fire drought severity is expected to increase over the next century, as average water-year cumulative moisture deficit is predicted to be between +2.0 and +3.0 SD of the current 30-year mean by the year 2050 (Westerling *et al.*, 2011). For comparison, during the most extreme and extended post-fire drought (2000–03) in our study period, the 3-year post-fire mean cumulative moisture deficit ranged from +0.7 to +1.1 SD of the 30-year mean. Together, this indicates that over the next century, large fire years followed by droughts at least as severe as those seen in recent decades will become a regular occurrence in the US Northern Rockies and similar systems. The combination of fire activity and drought could catalyse substantial biogeographical shifts in forest biomes (as suggested by Dobrowski *et al.*, 2015).

Based on our findings, one manifestation of the changes outlined above will be substantial compositional shifts in the tree species that dominate subalpine forests, as most species that currently dominate subalpine forests may be particularly challenged. The combined effects of larger burn patches and more severe post-fire drought is likely to favour species with higher drought tolerance and adaptations for wind dispersal and seed banking, such as fire evaders/invaders (e.g. lodgepole pine). In contrast, fire avoiders (e.g. Engelmann spruce and subalpine fir) are likely to become less common. The capacity for development of both serotinous and non-serotinous cones on lodgepole pine seedlings younger than 10 years (Turner *et al.*, 2007) can also buffer against predicted increases in fire frequency (Westerling *et al.*, 2011). Fire avoiders such as Engelmann spruce and subalpine fir, on the other hand, require several decades before they can produce cones (Burns & Honkala, 1990), leaving them additionally vulnerable to increases in fire frequency.

Where post-fire seedling establishment of subalpine tree species is reduced, establishment may increase for upper treeline or montane tree species. Slowly reproducing upper treeline pioneer species such as whitebark pine may benefit from a protracted establishment period and long-distance seed dispersal from birds. Together, these factors could provide a spatial and temporal buffer against larger patch sizes and post-fire drought, increasing the likelihood of seed arrival/germination during favourable conditions. Quaking aspen may benefit from increased fire frequency (Kulakowski *et al.*, 2013) and severity, owing to extremely light seeds that can be dispersed by wind over several kilometres (Turner *et al.*, 2003) and the ability to resprout from underground root structures once established. Fire resisters/invaders with moderate drought tolerance (e.g. Douglas-fir) may benefit from predicted increases in fire frequency if mature trees can persist and are not killed by severe fire. Western larch, on the other hand, is highly drought sensitive (Piñol & Sala, 2000), and this may lead to failed post-fire tree seedling establishment even if seed is available. Provided there is suitable dispersal into burned areas, Douglas-fir probably stands the best chance of increased post-fire establishment in the subalpine

zone because of lower drought sensitivity compared with other conifers (Piñol & Sala, 2000).

Our findings also suggest that a second, and arguably more important, manifestation of the aforementioned changes to climate and associated fire activity will be changes in forest structure and extent, as the compensatory effects described above will probably not offset sharp decreases in overall post-fire tree establishment (as suggested by Bell *et al.*, 2014b). For example, if our models for overall tree seedling establishment are extended to match the expected post-fire climate conditions of the mid-21st century (drought severity between +2.0 and +3.0 SD of our study period, but holding all other variables in our models constant at their means), post-fire tree seedling establishment would decrease by one to two orders of magnitude from the present-day rates we observed, and by three orders of magnitude from rates observed after the 1988 Yellowstone fires (Turner *et al.*, 2004). If future increases in fire activity also result in larger patch sizes (and thus greater distances to post-fire seed sources), post-fire seedling establishment would decline further. Such low levels of seedling establishment would likely lead to local regeneration failures and conversions from forest to non-forest vegetation.

Fire-prone subalpine and boreal forests are among the most extensive biomes world-wide. Evidence is already accumulating in support of changing climate, as well as a changing extent and patterns of fire in these systems (Westerling *et al.*, 2011; de Groot *et al.*, 2013), and the magnitude of drought severity and fire activity expected in the 21st century (Westerling *et al.*, 2011) far exceeds that found in the Holocene record (Whitlock *et al.*, 2003). Our findings are consistent with mechanisms that could lead to near- and mid-term future decreases in post-fire resilience, reductions in extent and increased patchiness of high-elevation and high-latitude forests.

ACKNOWLEDGEMENTS

We thank B. Weiland, C. Lane, O. Ituah, J. Ament and B. Gilmore for assistance with field data collection and/or data preparation. L. Westerling and J. Milostan provided access to the climate dataset. We thank H. Harlow, D. Abendroth, D. Divoky and T. Carolin from the NPS for assistance with logistics and field site access. S. Anderson assisted with statistical analysis. J. Williams, K. Raffa, E. Damschen, P. Townsend, B. Poulter, R. Field and two anonymous referees provided valuable feedback on earlier versions of this manuscript. This study was funded by a Graduate Research Innovation Award from the US Joint Fire Science Program (award no. 12-3-01-3) and a US National Park Service – George Melendez Wright Climate Change Fellowship.

REFERENCES

- Agee, J.K. (1993) Fire ecology of Pacific Northwest forests. Island Press, Washington, DC.
- Arno, S.F. (1980) Forest fire history in the Northern Rockies. *Journal of Forestry*, **78**, 460–465.
- Baker, W.L. (2009) Fire ecology in Rocky Mountain landscapes, 1st edn. Island Press, Washington, DC
- Barrett, S. (1994) Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. *International Journal of Wildland Fire*, **4**, 65–76.
- Barrett, S.W., Arno, S.F. & Key, C.H. (1991) Fire regimes of western larch–lodgepole pine forests in Glacier National Park, Montana. *Canadian Journal of Forest Research*, **21**, 1711–1720.
- Beers, T.W., Dress, P.E. & Wensel, L.C. (1966) Notes and observations: aspect transformation in site productivity research. *Journal of Forestry*, **64**, 691–692.
- Bell, D.M., Bradford, J.B. & Lauenroth, W.K. (2014a) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, **23**, 168–180.
- Bell, D.M., Bradford, J.B. & Lauenroth, W.K. (2014b) Mountain landscapes offer few opportunities for high-elevation tree species migration. *Global Change Biology*, **20**, 1441–1451.
- Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B. & Johnstone, J.F. (2013) The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, **63**, 866–876.
- Burns, R.M. & Honkala, B.H. (1990) Silvics of North America. Agriculture handbook 654. Vol 1 (conifers), US Department of Agriculture Forest Service, Washington, DC.
- 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. *Journal of Vegetation Science*, **21**, 472–487.
- 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: tree recruitment patterns in the western US. *Global Ecology and Biogeography*, **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 wild-fire in the Klamath Siskiyou Mountains. *Canadian Journal of Forest Research*, **39**, 823–838.
- Donato, D.C., Campbell, J.L. & Franklin, J.F. (2012) Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science*, **23**, 576–584.
- Freund, J.A., Franklin, J.F., Larson, A.J. & Lutz, J.A. (2014) Multi-decadal establishment for single-cohort Douglas fir forests. *Canadian Journal of Forest Research*, **44**, 1068–1078.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015) Boreal forest health and global change. *Science*, **349**, 819–822.

- Greene, D.F. & Johnson, E.A. (1996) Wind dispersal of seeds from a forest into a clearing. *Ecology*, **77**, 595–609.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.-J. (1999) A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, **29**, 824–839.
- de Groot, W.J., Flannigan, M.D. & Cantin, A.S. (2013) Climate change impacts on future boreal fire regimes. *Forest Ecology and Management*, **294**, 35–44.
- Harvey, B.J. (2015) *Causes and consequences of spatial patterns of fire severity in Northern Rocky Mountain forests: the role of disturbance interactions and changing climate*. PhD Thesis, University of Wisconsin–Madison.
- Harvey, B.J., Donato, D.C., Romme, W.H. & Turner, M.G. (2014) Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecological Applications*, **24**, 1608–1625.
- Johnstone, J.F., Chapin, F.S., III, Foote, J., Kemmett, S., Price, K. & Viereck, L. (2004) Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research*, **34**, 267–273.
- Johnstone, J.F., Chapin, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V. & Turetsky, M. (2010a) Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research*, **40**, 1302–1312.
- Johnstone, J.F., McIntire, E.J.B., Pedersen, E.J., King, G. & Pisaric, M.J.F. (2010b) A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. *Ecosphere*, **1**, art. 14.
- Kashian, D.M., Turner, M.G., Romme, W.H. & Lorimer, C.G. (2005) Variability and convergence in stand structural development on a fire-dominated subalpine landscape. *Ecology*, **86**, 643–654.
- Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G. & Ryan, M.G. (2006) Carbon storage on landscapes with stand-replacing fires. *BioScience*, **56**, 598–606.
- Kemp, K.B., Higuera, P.E. & Morgan, P. (2016) Fire legacies impact conifer regeneration across environmental gradients in the US Northern Rockies. *Landscape Ecology*, **31**, 619–636.
- Kipfmüller, K.F. & Baker, W.L. (2000) A fire history of a subalpine forest in south-eastern Wyoming, USA. *Journal of Biogeography*, **27**, 71–85.
- Kipfmüller, K.F. & Kupfer, J.A. (2005) Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness area. *Annals of the Association of American Geographers*, **95**, 495–510.
- Kulakowski, D., Matthews, C., Jarvis, D. & Veblen, T.T. (2013) Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). *Journal of Vegetation Science*, **24**, 168–176.
- Larson, A.J. & Franklin, J.F. (2005) Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. *Forest Ecology and Management*, **218**, 25–36.
- McKenzie, D.A. & Tinker, D.B. (2012) Fire-induced shifts in overstorey tree species composition and associated understorey plant composition in Glacier National Park, Montana. *Plant Ecology*, **213**, 207–224.
- Millar, C.I. & Stephenson, N.L. (2015) Temperate forest health in an era of emerging megadisturbance. *Science*, **349**, 823–826.
- Miller, J.D. & Thode, A.E. (2007) Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sensing of Environment*, **109**, 66–80.
- Minore, D. (1979) Comparative autecological characteristics of northwestern tree species – a literature review. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Morgan, P., Heyerdahl, E.K. & Gibson, C.E. (2008) Multi-season climate synchronized forest fires throughout the 20th century, Northern Rockies, USA. *Ecology*, **89**, 717–728.
- Morgan, P., Heyerdahl, E.K., Miller, C., Wilson, A.M. & Gibson, C.E. (2014) Northern Rockies pyrogeography: an example of fire atlas utility. *Fire Ecology*, **10**, 14–30.
- Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- Piñol, J. & Sala, A. (2000) Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. *Functional Ecology*, **14**, 538–545.
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Romme, W.H. & Despain, D.G. (1989) Historical perspective on the Yellowstone fires of 1988. *BioScience*, **39**, 695–699.
- Romme, W., Boyce, M., Gresswell, R., Merrill, E., Minshall, G., Whitlock, C. & Turner, M. (2011) Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems*, **14**, 1196–1215.
- Schoennagel, T., Turner, M.G. & Romme, W.H. (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology*, **84**, 2967–2978.
- Schoennagel, T., Veblen, T.T. & Romme, W.H. (2004) The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience*, **54**, 661.
- Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H. & Turner, M.G. (1994) Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research*, **24**, 897–903.
- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L. & Mellmann-Brown, S. (2001) Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology*, **82**, 2587–2600.
- Trumbore, S., Brando, P. & Hartmann, H. (2015) Forest health and global change. *Science*, **349**, 814–818.
- Turner, M.G. & Romme, W.H. (1994) Landscape dynamics in crown fire ecosystems. *Landscape Ecology*, **9**, 59–77.

- Turner, M.G., Hargrove, W.W., Gardner, R.H. & Romme, W.H. (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, **5**, 731–742.
- 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. *Ecological Monographs*, **67**, 411–433.
- Turner, M.G., Gardner, R.H. & Romme, W.H. (1999) Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire*, **9**, 21–36.
- Turner, M.G., Romme, W.H., Reed, R.A. & Tuskan, G.A. (2003) Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecology*, **18**, 127–140.
- 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). *Forest Ecology and Management*, **242**, 119–126.
- Urza, A.K. & Sibold, J.S. (2013) Nondestructive aging of postfire seedlings for four conifer species in northwestern Montana. *Western Journal of Applied Forestry*, **28**, 22–29.
- Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*. Springer, New York.
- Walker, B., Hollin, C.S., Carpenter, S.R. & Kinzig, A. (2004) Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society*, **9**, 5.
- Wan, H.Y., Olson, A.C., Muncey, K.D. & St. Clair, S.B. (2014) Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. *Forest Ecology and Management*, **329**, 59–68.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, **313**, 940.
- Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H. & Ryan, M.G. (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences USA*, **108**, 13165–13170.
- Whitlock, C., Shafer, S.L. & Marlon, J. (2003) The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *Forest Ecology and Management*, **178**, 5–21.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangogadamage, C., Cai, M. & McDowell, N.G. (2012) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, **3**, 292–297.

BIOSKETCH

Brian J. Harvey is a David H. Smith Postdoctoral Research Fellow in the Department of Geography at the University of Colorado – Boulder. His research focuses on forest disturbance ecology at spatial scales ranging from individual trees to landscapes and regions. Topically, his research asks questions to better understand the causes and consequences of natural disturbances (e.g. fire, insect outbreaks, drought) and how disturbances interact to shape forest ecosystems.

Editor: Ben Poulter