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LETTER

Evidence for declining forest resilience to wildfires under climate change

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Abstract

Forest resilience to climate change is a global concern given the potential effects of increased disturbance activity, warming temperatures and increased moisture stress on plants. We used a multi-regional dataset of 1485 sites across 52 wildfires from the US Rocky Mountains to ask if and how changing climate over the last several decades impacted post-fire tree regeneration, a key indicator of forest resilience. Results highlight significant decreases in tree regeneration in the 21st century. Annual moisture deficits were significantly greater from 2000 to 2015 as compared to 1985–1999, suggesting increasingly unfavourable post-fire growing conditions, corresponding to significantly lower seedling densities and increased regeneration failure. Dry forests that already occur at the edge of their climatic tolerance are most prone to conversion to non-forests after wildfires. Major climate-induced reduction in forest density and extent has important consequences for a myriad of ecosystem services now and in the future.

Keywords

Climate change, forest recovery, forest resilience, tree regeneration, wildfire.

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INTRODUCTION

Increased wildfire activity, in combination with global increases in temperature, drought and extreme weather (Jolly *et al*. 2015; Intergovernmental Panel on Climate Change 2016; Bowman *et al*. 2017) raise uncertainties about subsequent ecosystem responses (Turner 2010; Millar & Stephenson 2015). Forest resilience, or the capacity of a forest to return to a pre-disturbance state (Gunderson 2000), is strongly dependent on sufficient tree regeneration (Johnstone *et al*. 2016). Because temperature and drought stress disproportionally impact trees in their youngest life stages (seedlings and saplings) (Bell *et al*. 2014; Dobrowski *et al*. 2015), forest resilience to disturbances under warming climatic conditions remains highly uncertain.

Disturbance events, including wildfires, break the 'inertia' of existing communities and, under scenarios of climate change, allow for the development of new assemblages better suited to post-disturbance conditions (Donato *et al*. 2016). For example, interactions between wildfire and post-fire drought may decrease forest resilience through reduced conifer tree regeneration, potentially resulting in forest ecosystem conversion to persistent alternate shrub or grassland states or different tree species assemblages (Lenihan *et al*. 2008; Enright *et al*. 2015). Shifts in tree species distributions are expected with climate change (Allen *et al*. 2010; Petrie *et al*. 2017), particularly at the warmer, drier edge of species' ranges, and recent studies suggest that fire may be catalysing these changes throughout the Rocky Mountains and beyond (Donato *et al*. 2016; Rother & Veblen 2016; Welch *et al*. 2016).

Increased fire activity in the western US and in the US Northern Rockies has been driven by both rising temperatures and widespread drought, particularly since 2000 (Abatzoglou & Williams 2016; Westerling 2016; Fig. 1d). As temperatures continue to warm, regionally and globally, climate may become the dominant control on tree regeneration (Bell *et al*. 2014; Enright *et al*. 2015), resulting in regional changes in forest composition and extent. If suitable climate for post-fire tree recruitment is becoming increasingly rare, we expect the influence of climate to become increasingly important, relative to other factors limiting regeneration (e.g. seed availability, burn severity and competing vegetation).

Here, we conducted a meta-analysis of field measurements from 1485 sites that burned in 52 wildfires between 1988 and 2011 in temperate conifer forests of the US Rocky Mountains (Fig. 1a). We combined data on tree seedling presence and density from multiple recently published papers (Harvey *et al*. 2013; Wells 2013; Stevens-Rumann *et al*. 2014; Harvey *et al*. 2014a,b; Harvey *et al*. 2015; Morgan *et al*. 2015; Rother & Veblen 2016; Harvey *et al*. 2016; Kemp *et al*. 2016; Stevens-

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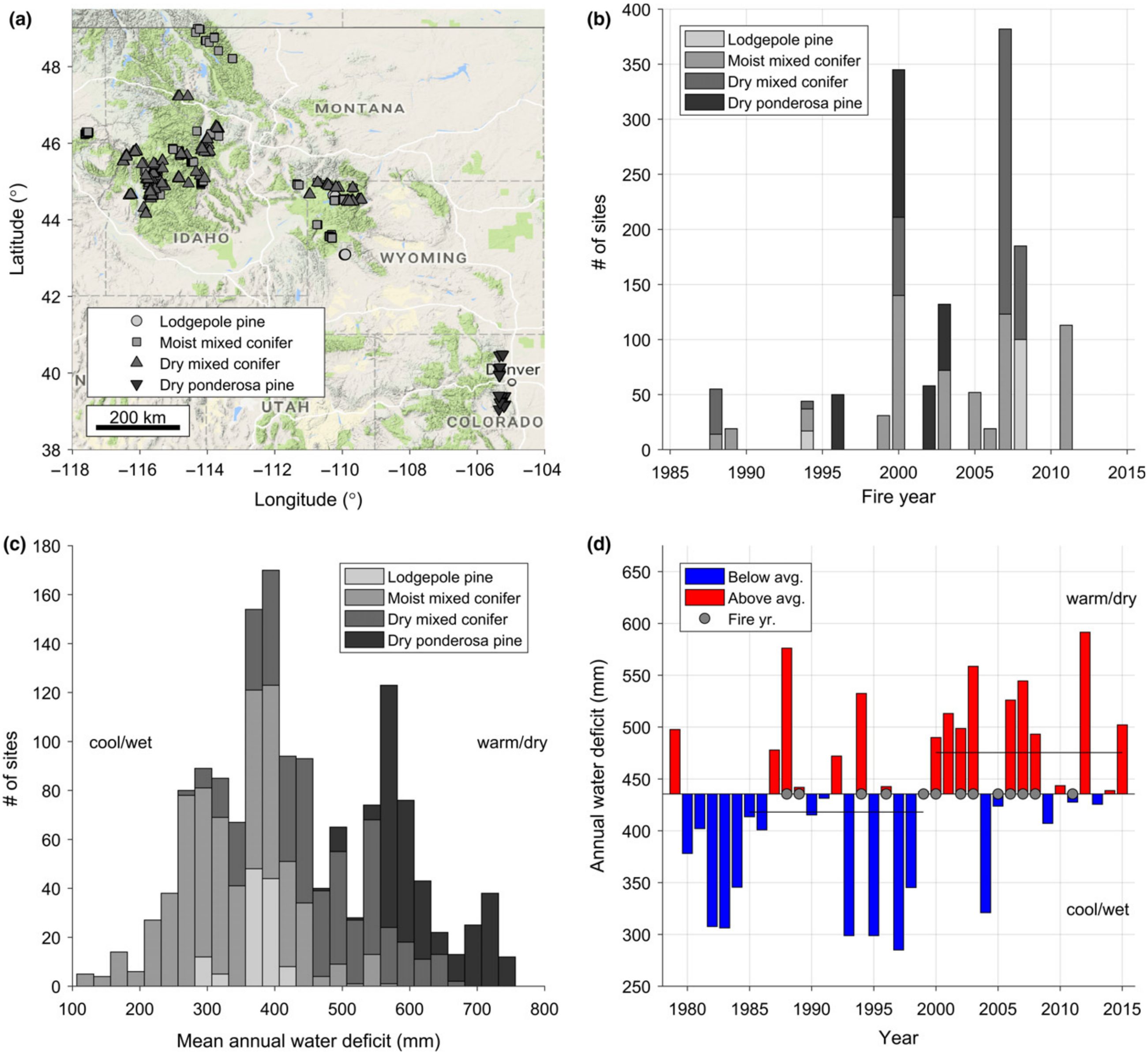

Figure 1 (a) The geographic location of sites used in this study. Black inverted triangles indicate dry ponderosa pine forests, dark grey triangles indicate dry mixed conifer forests, lighter grey squares indicate moist conifer forests, and the lightest grey circles indicate lodgepole pine forests. (b) Sites displayed by fire year and number from each fire year, with colours indicating forest type. (c) Mean annual water deficit of all sites, again coloured by forest type, with cool/wet sites on the right and warm/dry sites on the left. (d) The mean annual water deficit averaged across all sites, starting in 1979, before the period of analysis in this study (1985–2015). The black horizontal lines indicate the 1985–1999 and 2000–2015 mean values.

Rumann & Morgan 2016; Donato *et al.* 2016) with climate data to test the hypothesis that tree regeneration following wildfires is decreasing under the warmer, drier climate conditions of the 21st century. Specifically, we used this unique dataset to address three questions: (1) is there evidence of reduced tree regeneration following wildfires under the warmer, drier conditions of the 21st century compared to the cooler, wetter end of the 20th century, (2) what mechanisms are responsible for tree regeneration failures and (3) what forest types or regions are most vulnerable to forest loss due to the combined effects of wildfires and climate warming? Our results reveal how climate and climate changes strongly influences the response of forest ecosystems to disturbances, with important implications for long-term forest resilience and the ecosystem services of forested landscapes.

MATERIALS AND METHODS

Study domain

We analysed field data of tree seedling presence and density collected from 1485 sites that burned at mixed severity between 1988 and 2011, spanning a region of over 2 million km^2 and 13 degrees of latitude, and elevations from 692 to 2764 m above sea level. Within the US Rocky Mountains, sites range from Colorado to northern Idaho and Montana, with forest types ranging from low-elevation ponderosa pine (*Pinus ponderosa*) and dry conifer forests (including Douglas-fir, *Pseudotsuga menziesii,* and ponderosa pine), to moist conifer forests that include a mix of Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), various fir (*Abies*) species depending on location including white fir (*A. concolor),* subalpine fir (*A. lasiocarpa)* and/or grand fir *(A. grandis),* to forests consisting of pure lodgepole pine. Additional species found in low abundance (≤ 2.5% of all seedlings) across our study sites included whitebark pine (*Pinus albicaulis),* aspen *(Populus tremuloides)* and western larch (*Larix occidentalis)*. Burn severity was categorised both in the field and using satellite imagery derived relativised differenced normalised burn ratio (RdNBR). RdNBR ranged from 0 to 3907. These sites vary climatically with 30-year mean annual water deficits that range from 120 to 756 mm (Fig. 1). Due to the climatically similar conditions of moist mixed conifer and lodgepole pine sites, we combined these in our analysis, resulting in two distinct forest types for all analyses: 'dry conifer forests' and 'moist conifer forests'. We focus on this region because it is highly vulnerable to climate-induced increases in large wildfires (Dennison *et al.* 2014; Westerling 2016), and reduced post-fire tree regeneration is of particular concern (Donato *et al.* 2016; Harvey *et al.* 2016; Kemp *et al.* 2016; Rother & Veblen 2016).

Field methods and site-specific variables

Tree seedling data used in this analysis were collected on 1485 sites, ranging in size from 100 to 700 m^2, between 2010 and 2014, with methods described in detail in recent publications (Harvey *et al.* 2013; Wells 2013; Stevens-Rumann *et al.* 2014; Harvey *et al.* 2014a,b; Harvey *et al.* 2015; Rother & Veblen 2016; Kemp 2015; Harvey *et al.* 2016*;* Kemp *et al.* 2016; Morgan *et al.* 2015; Stevens-Rumann & Morgan 2016; Donato *et al.* 2016). All studies recorded tree seedling density by species, estimated pre-fire tree density, distance to nearest live seed source trees (m), tree mortality (%), burn severity (both RdNBR and field-verified low, moderate, or high tree mortality relative to pre-fire tree density at each site), aspect (degrees), slope (%), elevation (m) and latitude and longitude. Most studies (1183 out of 1485 sites, 80%) also estimated establishment year of seedlings based on counts of terminal bud scars. A heat load index from direct solar radiation was calculated using slope, aspect and latitude (following McCune & Keon 2002). We calculated site-specific burn severity as 100% tree mortality ('stand replacing') or < 100%. This decision was made due to varying methods of determining burn severity among the original studies. Areas that experienced post-fire harvesting or planting were excluded from the dataset.

Climate data

To quantify moisture stress for all analyses, we used water deficit, defined as the difference between actual evapotranspiration (AET) and potential evapotranspiration (PET; AET-PET, mm), although in general, our results were robust to using varying water balance metrics (i.e. ratio of AET/PET, AET or PET). Climate data from 1979 to 2015 were compiled using 800-m PRISM data (through 2009) and ancillary wind and topographically corrected solar radiation data from gridMET (4 km resolution; Abatzoglou 2013). Time series data after 2009 were generated by taking baseline PRISM data and superposing anomalies from 4-km climate layers using climatologically aided interpolation (Abatzoglou 2013). Reference evapotranspiration was calculated using the Penman–Monteith approach for a grass reference surface, and we used the water balance algorithms of Dobrowski *et al.* (2013). We created an average 30-year annual water year deficit (1985–2015) for each site (hereafter, 'average site climate'). We quantified post-fire climate by first calculating the Z-score for a site-specific time series of water deficit, and then taking the average Z -score in years 1–3 after each fire (Harvey *et al.* 2016); we termed this metric 'post-fire relative water deficit'. Using a Z -score, this index quantifies post-fire climate relative to the average climate at each site, where 0 indicates average conditions, and positive (negative) values indicate warm/dry (cool/wet) post-fire conditions. Based on the time series of water deficit across our study region, which displays an increasing moisture deficit towards present, we conducted our analyses with data stratified into two time periods: wildfires that burned before 2000 vs. during or after 2000. This date was chosen based on the dominance of drier conditions since 2000, which has been demonstrated region-wide (Fig. 1d; Abatzoglou & Williams 2016). There was a 14% increase in deficit between the 1985–1999 and 2000–2015 time periods, and no other break point in the data resulted in a larger difference in deficit.

Sensitivity analysis

Given the potential influence of time-since-fire on our results (i.e. some sites may not have had enough post-fire years to achieve the same cumulative seedling densities), we conducted analyses to account for varying times-since-fire values among sites. First, utilising the estimated age of individual seedlings from terminal bud scars, we stratified our data by year of seedling establishment to analyse if the proportion of sites exceeding recruitment thresholds between time periods was sensitive to time-since-fire. We did this first for only trees that established in the first year, then first two, then five and then 10 years post-fire, and for each iteration, we limited the entire dataset to sites with time-since-fire values that exceeded this minimum time-since-fire value. For example, for one analysis, we included only those seedlings that established within the first 5 years post-fire, and excluded all sites where time-since-fire was less than 5 years. We conducted a Pearson's Chi-squared test on the effect of 'time period' at each of these time-since-fire thresholds (Table S1).

Second, using the estimated establishment years of tree seedlings from sites in our oldest fires (1988–1994), we examined tree seedling accumulation curves for each species to estimate the point at which most tree seedlings are recruited to a site (Fig. 2). Specifically, we qualitatively assessed temporal patterns of post-fire tree seedling establishment by plotting the number of seedlings established in each year over time, as well as the cumulative seedling establishment over time. Assigning ages to conifer seedlings using bud scar counts is only accurate to within approximately 2–3 years of the true seedling age, and only for trees under 20 years of age, depending on species (Urza & Sibold 2013). As we did not perform destructive sampling to verify bud scar counts, our estimates of seedling establishment dates were used to qualitatively assess temporal patterns in post-fire establishment; we did not use estimated establishment dates quantitatively to assess differences between the two time periods (i.e. pre- and post-2000).

Statistical analyses

To examine the role of climatic and site-specific factors on seedling abundance, we developed a recruitment threshold for evaluating the likelihood that each site would eventually reach the density of the pre-burn forests. Tree seedling densities are typically highly skewed, requiring analysis methods that can accommodate non-normal distributions (e.g. Poisson, Gamma; Kemp *et al.* 2016; Harvey *et al.* 2016). Given the high variability in the seedling densities across the 1425 sites with pre-fire stand density estimates, we created a binomial response based on pre-fire tree densities at each site. We assigned each site a ‘1’ if it had an equal or greater number of seedlings than the number of pre-fire trees, and a ‘0’ if it had fewer, creating a binomial model for subsequent analysis. This criterion is simple and site-specific, and it does not account for (unknown) rates of seedling mortality, pre-fire tree density or age structure or whether seedlings will continue to establish. All of these factors are unknown and likely vary across sites and forest types (see Lutz & Halpern 2006). Planting guidelines or stocking rates were ruled out for the purposes of this threshold because (1) information was outdated or lacking from some National Forests, (2) 312 of our sites are managed by agencies that do not use silvicultural guidelines (e.g. National Park Service and city public lands) and (3) there is high variability in species composition and productivity across our sites, which would impact the applicability of those guidelines (Welch *et al.* 2016). Due to the high mortality typically observed in tree seedlings, and particularly in young age classes (Calvo *et al.* 2013; Larson *et al.* 2015), we used a Pearson Chi-squared test, in JMP (SAS Institute Inc. 2007), to evaluate the sensitivity of our results to different recruitment thresholds. We tested the assumption that pre-fire stand densities would be reached when seedling densities exceeded 50, 75,

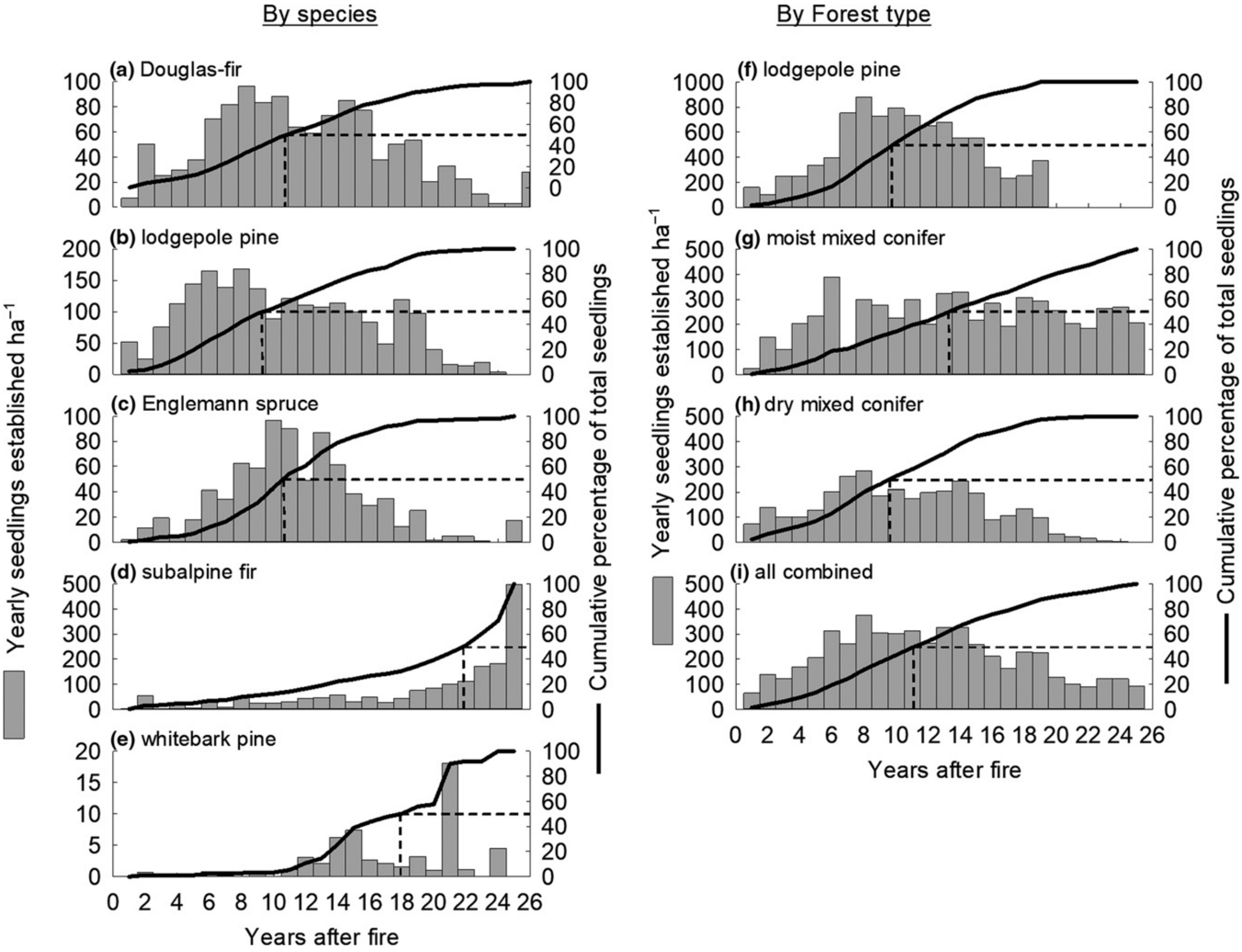

Figure 2 Tree seedling accumulation curves for each species (left column) and by forest type (right column). Data are only from fires that burned from 1988-1994 and establishment year was approximated using bud scar counts. Black dashed line indicates the time at which 50% of recruitment occurs.

Table 1 Generalised linear mixed model (GLMM) results for predicting sites achieving pre-fire tree recruitment thresholds

	Estimate	Std. Error	Z value	P
Pre-2000[1]				
(Intercept)	**−15.48**	**6.68**	**−2.317**	**0.020**
30-year water deficit	**0.018**	**0.008**	**2.354**	**0.019**
3-year post-fire deficit Z-score	**−15.64**	**4.23**	**−3.695**	**0.0002**
Stand-replacing fire	−0.434	0.521	−0.832	0.405
Heat load index	**15.54**	**7.22**	**2.152**	**0.031**
Minimum distance to seed source	**−0.007**	**0.003**	**−2.109**	**0.035**
30-year water deficit x 3-year post-fire deficit Z-score	**0.029**	**0.010**	**2.699**	**0.007**
Post-2000[2]				
(Intercept)	1.696	1.016	1.669	0.095
30-year water deficit	**−0.004**	**0.001**	**−3.793**	**0.0001**
3-year post-fire deficit Z-score	−2.024	1.101	−1.838	0.066
Stand-replacing fire	−0.120	0.181	−0.667	0.505
Heat load index	1.074	0.913	1.177	0.239
Minimum distance to seed source	**−0.001**	**0.001**	**−3.412**	**0.0006**
30-year water deficit x 3-year post-fire deficit Z-score	0.003	0.002	1.295	0.195

1Pre-2000 the random effect of the 7 individual fire events had a variance of 40.9 and a standard deviation of 6.4.

2Post-2000, the random effect of the 42 individual fire events had a variance of 2.7 and a standard deviation of 1.6.

Displayed are estimates, standard errors, Z values and P values for fixed effects of the GLMM on tree seedling densities achieving pre-fire tree density. Those in bold are significant at $\alpha = 0.05$

100, 125, 150 or 200% of pre-fire tree density (results in Table S2).

We fit a binomial generalised linear mixed model (GLMM) with a logit-link using the 100% recruitment threshold as our binomial response. The models were fitted using fixed effects representing average site climate (30-year average water deficit, [AET-PET, mm]), post-fire relative water deficit (3-year post-fire average water deficit, expressed as a Z-score calculated with the 1985–2015 values) and the interaction between the two, as well as site-specific effects for heat load index, burn severity (100% tree mortality vs. 0–99%) and distance to seed source (m). We set each individual fire event as a random effect to account for potential spatial autocorrelation between sites in individual fires and variability due to burning condition, and specific post-fire conditions. We performed this analysis across all fire years for sites burned prior to 2000, and sites burned during or after 2000. We considered previous disturbance, either fire or bark beetle, as a potential additional fixed effect. This factor was excluded from the final models as no sites burned before 2000 had a known previous disturbance in the past 30–50 years, and after 2000 those previous disturbances that were quantified were non-significant in the model. Analysis was conducted on the site level ($N_{total} = 1485$) and significance was assessed at the $\alpha = 0.05$ level. This analysis was performed in R version 3.2.5 (R Development Core Team 2011) with the *lme4* (Bates *et al.* 2015), *car* (Fox & Weisberg 2011) and *effects* (Fox 2003) packages. The GLMM model fit was assessed using the area under the Receiver Operating Curve (AUC), where values of 0.5 indicate a model no different from random and a value of 1.0 indicates perfect accuracy. To ensure that our sites and post-fire site conditions did not vary significantly between time periods, we conducted Pearson's Chi-squared tests, t-tests or rank sum tests (depending on conformity to normality assumptions) on all variables considered for our GLMM, grouped by time period.

To understand which forests were most vulnerable to the recent climatic changes, we examined both tree seedling presence and recruitment thresholds. For seedling presence/absence analyses, we classified presence of one or more seedlings with a '1'. We used presence/absence data in a Pearson's Chi-squared test to assess the effect of deficit, forest type and time period on seedling presence. Given the variability in plot size across forest types and studies (i.e. site size varied between 100 and 700 m^2), we did not conduct a GLMM on presence/absence data, because we believed it would bias results due to area sampled. Then, we conducted a Chi-squared analysis to determine which forest types experienced the greatest degree of change in regeneration during the two time periods analysed. We also compared the proportion of sites that met the regeneration threshold in the two forest types (dry conifer and moist conifer).

RESULTS

Tree regeneration was significantly reduced following fires that occurred in the early 21st century relative to fires that

Table 2 Results from comparisons of site-specific variables between the two time periods

Factor	Statistic	P	20th century	21st century
Minimum distance to seed source (m)	$\chi^2 = 0.46$	0.50	62 (100)	71 (104)
Elevation (m)	$F = 0.54$	0.46	2007 (377)	1993 (427)
Slope (degree)	$F = 10.18$	**0.0014**	21 (16)	26 (20)
Aspect (degree)	$F = 3.81$	0.06	167 (101)	183 (110)
Forest type (% of dry forest types)	$\chi^2 = 6.50$	0.08	49	52
Field-verified burn severity	$\chi^2 = 4.30$	0.23	10	15
(Categories: Low, Moderate,			22	22
high % of each)			68	63
Plot size (m^2)	$F = 0.13$	0.71	215 (14)	221 (5.6)
30-year climatology (mm)	$F = 0.57$	0.45	462 (132)	456 (120)
3-year post-fire relative water deficit (Z-score)	$F = 312.42$	**< 0.001**	−0.37 (0.57)	0.42 (0.45)

Depending on the variable, we conducted a Pearson's Chi-squared analysis, a rank sum test, or an ANKOVA on site-specific variables. Values in the right two columns are means (standard deviations), and those in bold indicate a significant difference between periods at $\alpha = 0.05$.

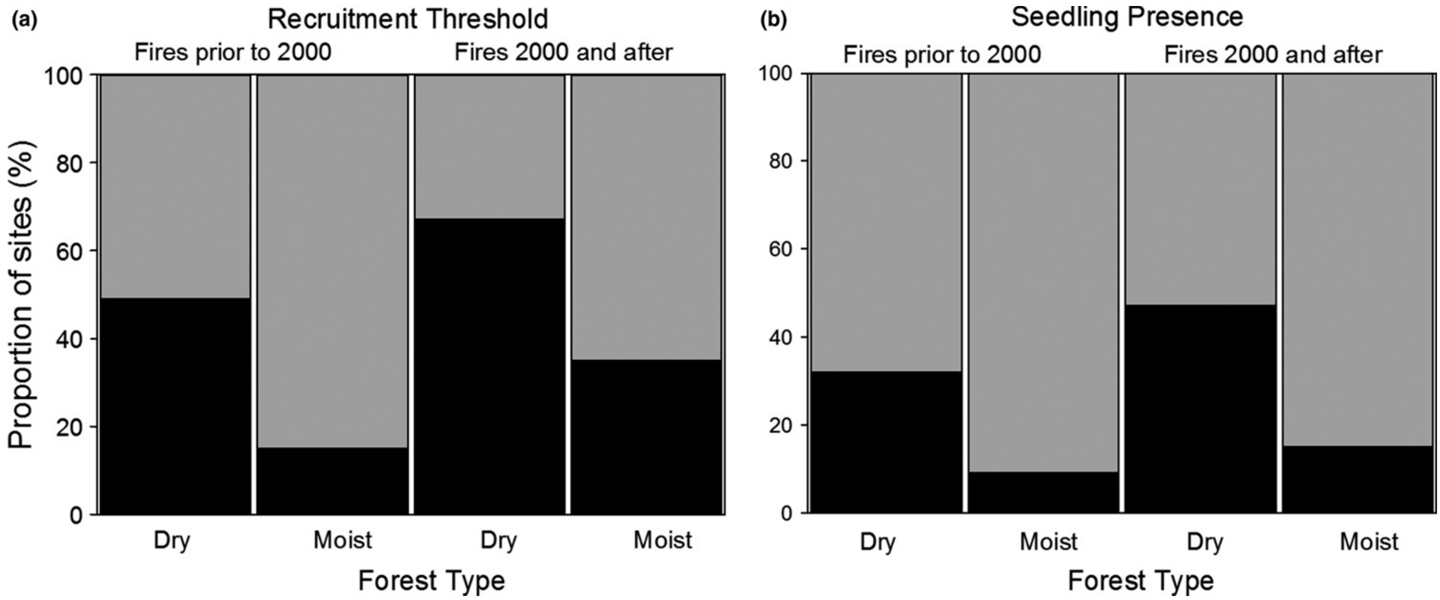

Figure 3 Displayed are the proportion of sites within each forest type [dry conifer (dry) and moist conifer (moist)] that (a) met recruitment thresholds for replacement (1; light grey) or not (0; black) and (b) had at least one conifer seedling present on a site. In both (a) and (b) we contrasted fires that occurred in the 20th century (left) and in the 21st century (right). Proportional differences between time periods (before 2000 or since 2000) were compared using a Pearson's Chi-squared test across all forest types in (a) and (b) and within dry forest and moist forests. All differences between time periods were significant ($\chi^2 > 7.4$, $P < 0.001$). [Correction added on 18 January 2018, after first online publication: the Figure 3 has been corrected]

occurred in the late 20th century. For sites burned at the end of the 20th century vs. the first decade of the 21st century, the proportion of sites meeting or exceeding pre-fire tree densities (e.g. recruitment threshold of 100%) decreased by nearly half (from 70 to 46%) and the percentage of sites experiencing no post-fire tree regeneration nearly doubled (from 19 to 32%; $\chi^2 > 15$, $P < 0.001$, Figs 3 and 4d).

Average site climate and distance to seed source were the two significant predictors of whether site-level seedlings densities exceeded recruitment thresholds needed to achieve pre-fire tree densities across both time periods (GLMM, Table 1). In addition to site-level characteristics (e.g. distance to seed source, heat load index and burn severity), average site climate, post-fire relative water deficit and the interaction between these two climate variables were significant drivers of seedling densities in areas burned prior to 2000. In contrast, for fires in the 21st century, post-fire relative water deficit and heat load index were no longer statistically significant predictors of post-fire tree regeneration. During this later period, tree regeneration was influenced only by average site climate and distance to seed source (Table 1). Overall, our models explain a significant portion of the variability in the post-fire recruitment threshold (pre-2000 GLMM AUC = 0.91; post-2000 GLMM AUC = 0.86). The random variables of fire event was included in the model pre-2000, as it reduced the AIC value from 204.4 to 180.6, and it increased GLMM AUC from 0.79 to 0.91. Post-2000 similar differences were detected in the model with the inclusion of the random effect, with AIC value decrease from 1554.0 to 1284.0 and GLMM AUC increase from 0.71 to 0.86.

Prior to 2000, post-fire relative water deficit had a negative effect on recruitment thresholds and heat load index had a positive effect. The interaction of post-fire relative water deficit and average site climate was observed prior to 2000, indicating that the effect of moist post-fire years more strongly influenced regeneration on wet sites compared to dry sites (Fig. S1a). However, given wide confidence intervals and small effect size, we do not interpret this interaction to be meaningful. In wildfires burned since 2000, post-fire relative water deficit was no longer a significant driver and as a result, the effect of moist post-fire years remained consistent across all average site climates (Fig. S1b). In both time periods, the effect of distance to seed source was negative. However, in contrast to the pre-2000 period, tree regeneration in wildfires that burned since 2000 was negatively related to average site climate.

Less tree regeneration occurred across all forest types in the 21st century. Among dry forest sites that burned prior to 2000, 68% had seedlings of any species present; this decreased significantly to 53% among dry forest sites that burned since 2000 (Fig. 2, $\chi^2 = 8.5$, $P = 0.004$). The proportion of dry forest sites with seedling densities exceeding recruitment thresholds was also lower after 21st-century wildfires, declining from 49% (in sites that burned prior to 2000) to 30% (in sites burned since 2000; $\chi^2 = 14.3$, $P = 0.0002$). Moist forest types exhibited a similar decline in regeneration ($\chi^2 > 7.5$, $P < 0.01$), but the proportion of sites with seedlings or densities exceeding recruitment thresholds was greater than 65% in both time periods, declining from 91 to 65%.

We tested several assumptions and potentially confounding factors in our analyses including variations in site conditions, the regeneration threshold created for our GLMM and the effect of time-since-fire on tree establishment. In our analyses of sites and post-fire site conditions between the two time periods, only slope and post-fire relative water deficit varied significantly between these periods (Table 2). Distance to seed

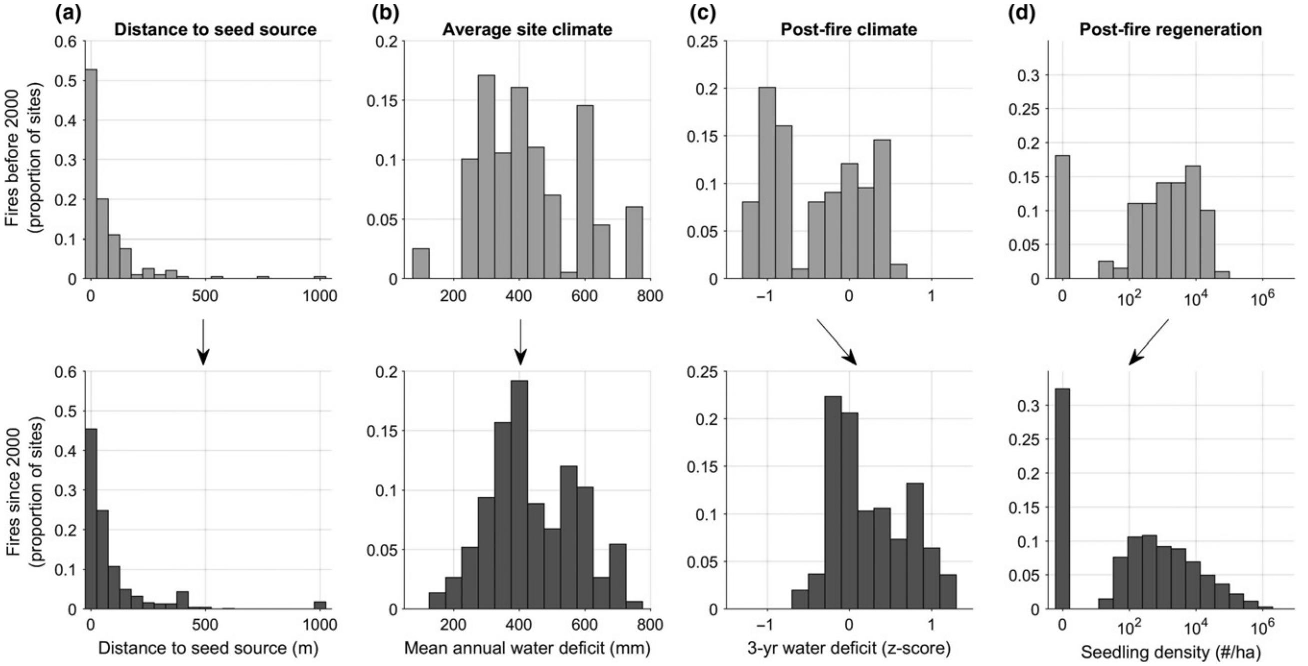

Figure 4 Displayed are site characteristics and tree seedling density from sites that burned before 2000 (light grey, top) and since 2000 (dark grey, bottom): (a) distance to seed source, (b) site climate using 30-year mean annual water deficit, (c) post-fire climate conditions using Z – scores of 3-year water deficit, and (d) post-fire regeneration as a function of seedling density. Vertical arrows indicate no general trends between time periods (before 2000 and since 2000) and diagonal arrows indicate significant directional shifts between time periods.

source, elevation, aspect, plot size, forest type and average site climate remained relatively constant across our time periods ($P > 0.05$). Sampled sites had slopes on average five degrees steeper in fires that burned in the 21st century compared to those burned in the 20th century ($F = 10.18$, $P = 0.0014$). Post-fire relative water deficit was significantly drier in the 21st compared to the end of the 20th century ($F = 312.42$, $P < 0.0001$, Fig. 4). Changing the regeneration threshold (i.e. from 50 to 200% of pre-fire stand density) did not change the significance of our results, and the majority of sites remained either below or above the threshold regardless of these changes (Table S2).

Our results were robust to the effects of varying time-since-fire, demonstrated by our analyses on seedling age and seedling establishment patterns. Regardless of time-since-fire establishment window, 1–10 years post-fire, the wildfires in the 21st century had significantly fewer sites with seedlings and significantly fewer sites meeting the recruitment threshold (Table S1). Across our oldest sites (fires from 1988 to 1994), seedling establishment in the first 3 years was highly predictive ($r^2 = 0.76$, Fig. S2) of tree densities 19–23 years post-fire, which is consistent with other studies within the region (Donato *et al.* 2016; Turner *et al.* 2016). Additionally, greater than 50% of tree seedling establishment across all species occurred within the first 10 years (Fig. 2). This was true for most of the dominant species we were able to assess, including lodgepole pine, Englemann spruce and Douglas-fir. However, this was not true for the more shade-tolerant species that were less abundant across all our sites, including whitebark pine and subalpine fir which will likely continue to establish for many decades post-fire.

DISCUSSION

Significantly less tree regeneration is occurring after wildfires in the start of 21st century compared to the end of the 20th century, and key drivers of this change were warmer and drier mean climatic conditions. Our findings demonstrate the increased vulnerability of both dry and moist forests to climate-induced regeneration failures following wildfires. The lack of regeneration indicates either substantially longer periods of forest recovery to pre-fire tree densities, or potential shifts to lower density forests or non-forest cover types after 21st-century wildfires (Millar & Stephenson 2015).

Trends of increasing temperature and associated water stress suggest that post-fire windows with suitable climate for tree seedling establishment and survival will occur less frequently in upcoming decades. Annual climate conditions have become warmer and drier throughout our study period (Fig. 1d), and it is likely that this shift is at least partially responsible for the observed decreases in tree regeneration (e.g. Little *et al.* 1994; Gray & Spies 1997; Savage *et al.* 2013; Rother *et al.* 2015). Our findings are not an artefact of varying characteristics of sites that burned before or since 2000, as forest type, burn severity, topography, mean distance to seed source and average site climates did not vary significantly between sites that burned during these two time periods (Table 2, Fig. 4). Although slope was significantly steeper at sites burned in the 21st century, the mean slope increase of five degrees is likely not ecologically meaningful. In contrast, post-fire water deficits increased from an average of −0.37 standard deviations below the mean to 0.25 standard deviations above the mean (Z-scores, relative to 1985–2015 average site climates), a trend that is consistent with regional and global warming documented since the 1970s (Mote & Salathe 2010; Fig. 1d mean lines). The absence of any cool/wet 3-year post-fire periods (i.e. water deficits more than 0.6 standard deviations below average; Fig. 4c) may explain why this variable was no longer a significant predictor of post-fire tree regeneration in the 21st century. However, the observed reductions in tree regeneration may also be attributable to other factors not assessed here, including the impacts of forest pests and pathogens, declining abundance of moisture-sensitive fungal symbionts or changes to other species i (Brown & Vellend 2014).

Distance to seed source and average site climate were the only two variables consistent across time periods in significantly predicting post-fire regeneration across our broad study region. These results are consistent with previous studies conducted at finer spatial scales and across fewer fires (Donato *et al.* 2009; Haire & McGarigal 2010; Harvey *et al.* 2016; Kemp *et al.* 2016), highlighting the importance of seed availability and climate in influencing post-fire seedling recruitment across broad spatial extents.

Our results further suggest that drivers of post-fire tree seedling occurrence and density changed from the 20th century to the 21st century, especially as climate in our study region became significantly warmer and drier than in prior decades (Fig. 1d). Tree regeneration following wildfires that burned prior to 2000 was greater at warmer, driers sites, but facilitated by post-fire periods with cooler, wetter annual climate conditions. The negative relationship between tree regeneration and average site climate in wildfires burned since 2000 indicate more favourable conditions for regeneration at sites that are on average cooler and/or wetter. This negative relationship demonstrates the potential increased vulnerability and lack of resilience on hotter and drier sites, or of dry forest species, to climate warming (e.g. Johnstone *et al.* 2016; Rother & Veblen 2016). The lack of importance of post-fire relative water deficit and heat load index is consistent with our expectation of warming overriding other controls of post-fire tree regeneration under directional climate warming, wherein windows of cooler, wetter conditions either no longer occur or are not sufficient to facilitate regeneration to pre-fire levels.

Our 23-year-study period is short compared to the time span of ecological succession in these ecosystems, and the longer term successional trajectories of these study sites are ultimately unknown. Particularly for sites that burned in the 21st century, sampling took place less than 15 years after wildfires, raising the possibility that recent lower tree regeneration could be an artefact of short post-fire sampling windows. However, two factors suggest this is unlikely. First, our sensitivity analysis of our recruitment thresholds (50–200% of pre-fire tree densities, Table S2) demonstrates that most sites either have an abundance of seedlings or close to none, with very few with seedling densities near the recruitment thresholds. For example, across fires that burned in the 20th century, 70% of sites that did not meet the recruitment threshold by 2 years post-fire (based on seedling age) also did not meet the recruitment threshold 10 years post-fire. Second, seedlings abundance or lack thereof in the first 2–3 years was highly predictive of long-term establishment trends. Due to the limited observed time since fire, especially for wildfires since 2000, we cannot state conclusively if sites with few or no tree seedlings are simply experiencing a delay in regeneration and will ultimately be forested, or if we are observing a more permanent shift to non-forested cover types. Tree seedlings may establish in response to short-term anomalous wetter periods in the future, but our results highlight that such conditions have become significantly less common since 2000, and they are expected to be less likely in the future (Enright *et al.* 2015). Further, persistent or long-lasting vegetation changes following wildfires have been observed worldwide, including North American boreal forests (Johnstone & Chapin 2006), temperate forests of New Zealand and southern South America (Kitzberger *et al.* 2016) and temperate rainforests in Tasmania (Holz *et al.* 2015).

Climate drives changes in ecosystem recovery after fire

Climate change is already affecting multiple ecosystem properties, leading to shifts in species composition and state changes (Walther *et al.* 2002; Donato *et al.* 2016). In the US Rocky Mountains, we documented a significant trend of reduced post-fire tree regeneration, even over the relatively short period of 23 years covered in this analysis. Our findings are consistent with the expectation of reduced resilience of forest ecosystems to the combined impacts of climate warming and wildfire activity. Our results suggest that predicted shifts from forest to non-forested vegetation (e.g. Bell *et al.* 2014) may be underway, expedited by fire disturbances (Kemp 2015; Donato *et al.* 2016; Harvey *et al.* 2016; Johnstone *et al.* 2016; Rother & Veblen 2016).

Regeneration failures, as measured by both seedling presence/absence and regeneration thresholds, occurred across all forest types (Figs 3 and 4d). Low-elevation forests, dominated by tree species near the warm, dry edge of their climatic tolerance may be particularly vulnerable to shifts to non-forest vegetation, because of the absence of any tree species that could reestablish under warmer, drier conditions (Harvey *et al.* 2016). Meanwhile, moist forest types may experience a shift in species dominance and a decrease in tree density. And while only 15% of the moist forest sites we studied lacked seedling after 21st-century fires, 35% of these sites did not meet the recruitment threshold. This represents a substantial increase (300%) relative to the 1985–1999 period, highlighting the impacts of warming in moist forests as well. Thus, unlike the potential transition from forest to non-forested cover types in low elevation, dry forests, moist forests may be more likely to experience a shift in forest structure or changes in species composition. Our study demonstrates that short post-fire periods of wetter climate that have favoured tree regeneration in the past may not occur frequently enough to facilitate tree regeneration in the future, across a broad region and multiple forest types in the Rocky Mountains. As scientists, managers and the public aim to understand and plan for increasing fire activity, our results suggest a high likelihood that future wildfires will facilitate shifts to lower density forest or non-forested states under a warming climate.

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AUTHOR CONTRIBUTIONS

CSSR is a CO-PI on the primary funding source, and she also collected and compiled field data, wrote the manuscript, organised meetings among all co-authors and conducted analyses. KBK is a CO-PI on the primary funding source, and she also collected and compiled field data, conducted analyses and contributed to manuscript editing and manuscript preparation. PEH compiled climate data, conducted analyses and contributed to manuscript editing. He also obtained funding for one of the initial data collection efforts. BJH collected and compiled field data, conducted background analyses and contributed to manuscript editing and manuscript preparation. MTR collected and compiled field data, contributed to manuscript editing and manuscript preparation. DCD collected and compiled field data contributed to manuscript editing and manuscript preparation. PM is the PI on the primary funding source for this project, and also obtained funding for several of the initial data collection efforts. PM also compiled field data and contributed to manuscript preparation. TTV contributed to manuscript editing and manuscript preparation, and obtained funding for one of the initial data collection efforts.

DATA ACCESSIBILITY STATEMENT

All data will be publicly available via archives of the Rocky Mountain Research Station with links from Fire Research and Management Exchange System (FRAMES; www.frames.gov).

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SUPPORTING INFORMATION

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