

FINAL REPORT

Climate variability and post-fire forest
regeneration in the Northern Rockies

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List of Abbreviations/Acronyms

BRT – Boosted Regression Trees

CA - Northern California

CO - Colorado Front Range

dNBR – differenced Normalized Burn Ratio

FACTS – Federal Activity

MTBS – Monitoring Trends in Burn Severity

NR - Northern Rockies

SW – Southwestern SU

VPD – Vapor Pressure Deficit

VWC – Volumetric water content

Keywords

climate, Douglas-fir, fire-catalyzed, ponderosa pine, post-fire, tree regeneration, vegetation transition

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Abstract

This project combined field sampling and statistical modeling to understand how interannual climate variability impacts forest regeneration at lower treeline, and how climate and fire interact to alter post-fire vegetation trajectories. Our findings are published in two primary and five secondary papers, which we summarize in this final report.

We used dendrochronology to identify annual establishment dates for 2820 destructively sampled ponderosa pine and Douglas-fir seedlings and saplings from 90 plots in 33 fires from four regions in the western US. We compared the establishment dates to seasonal climate conditions such as spring and summer soil moisture, summer vapor pressure deficit, and maximum surface temperature to quantify the relationship between seasonal climate and post-fire ponderosa pine and Douglas-fir regeneration. We found that regeneration had a nonlinear response to seasonal climate conditions, with distinct thresholds for recruitment, and that at dry sites across our study region, seasonal climate conditions over the past 20 years have crossed these thresholds, such that conditions have become increasingly unsuitable for regeneration. High fire severity and low seed availability further reduced the probability of postfire regeneration.

In a second study, we used the relationship between seasonal climate conditions and post-fire recruitment to project the probability of post-fire ponderosa pine and Douglas-fir regeneration, if a fire were to occur, across the Rocky Mountains from 1980-2014, and for a future climate scenario of a global mean increase in temperature of 2°C. Projections show that the area with climate conducive for post-fire regeneration of these two species has declined in recent years, with further declines expected in upcoming decades. By comparing projections to existing spatial data predicting the probability of stand-replacing fire, we highlight areas vulnerable to fire-catalyzed vegetation shifts due to a high risk of stand-replacing fire and low likelihood of post-fire regeneration. Across the study region, 6% and 4% of the area was vulnerable to fire-catalyzed shifts in the 1980s, for ponderosa pine and Douglas-fir, respectively. These numbers increased to 16% (ponderosa pine) and 10% (Douglas-fir) under future climate conditions. Our results highlight the potential for the combined influences of climate warming and an increase in wildfire activity to impact forest ecosystems through fire-catalyzed vegetation shifts.

Results from this project have direct implications for management strategies aimed at maintaining ponderosa pine and Douglas-fir forests in the US Rocky Mountains. For example, within most regions, particularly in the northern Rockies, we expect that some areas will retain climate suitable for post-fire regeneration of these two species, even under the +2°C future climate scenario. In these areas with suitable climate but where a seed source is lacking, post-fire management can focus on reforestation. In areas where climate is marginal for post-fire regeneration, managers conducting post-fire planting to maintain ponderosa pine and Douglas-fir on the landscape may need to consider novel and emerging reforestation tactics to boost success rates. In areas where climate is unsuitable for regeneration, managers may choose to emphasize pre-fire efforts to limit the occurrence of high severity fire and/or the size of stand-replacing patches. In areas with high risk of high severity fire and low likelihood of post-fire regeneration, managers may need to weigh the acceptability of a vegetation transition versus the potentially high costs of mitigation.

1. Objectives

The objective of this project were to understand how interannual climate variability impacts forest regeneration at lower treeline, and how climate and fire interact to alter post-fire trajectories. The original proposal had three main objectives:

- (1) Quantify the relationship between inter-annual climate variability and seedling establishment and survival for two dominant tree species at lower treeline (ponderosa pine and Doug-fir) in the Northern Rockies.**
- (2) Develop a simple landscape scale simulation model that represents post-fire tree regeneration as a function of seed availability, topography, and annual climate.**
- (3) Apply the simulation model from objective 2 to evaluate a suite of scenarios representing alternative future states, accounting for changes in climate, fire, and management activities.**

We addressed Objective 1 directly and expanded it to include additional study regions in Colorado, the Southwest, and northern California. We did not create the simulation model described in Objectives 2 and 3 because, after further discussions with managers, we decided it may not be as useful as other tools to which we could directly inform. We replaced Objective 2-3 by collaborating on the creation of a freely available tool, still under development, that predicts the probability of post-fire conifer regeneration in specific fires (30-m resolution) to help managers assess and prioritize post-fire reforestation needs. This “[RegenMapper](#)” tool is developed by USFS ecologist Zachary Holden, and now directly includes the climate-regeneration relationship we quantified through this work.

By assessing the implications of changing climate and fire regimes for post-fire forest regeneration, our study links directly to the task statement on “Implications of changing ecosystems – Northern Rockies.” If synergies between climate and fire severity result in a shift to non-forest dominated states, fuels and fire regimes will be greatly altered. Our results have clear implications for pre- and post-fire restoration strategies under current and future climate conditions by highlighting where natural post-fire conifer regeneration is unlikely and where vulnerability to post-fire vegetation transitions is high.

2. Background

Climate change has caused an increase in annual area burned, average fire size, and fire severity in the western US (Abatzoglou and Williams 2016; Parks and Abatzoglou 2020). Increases in fire activity, combined with increasingly warm and dry post-fire conditions, may undermine the mechanisms making Western forests resilient to wildfire, potentially resulting in fire-catalyzed vegetation shifts (Johnstone et al. 2016, Davis et al. 2018). Changes to forest ecosystems, including transitions to non-forest vegetation types, will significantly impact the ecosystem services and economic value provided by conifer forests in the western US.

Seedlings are particularly sensitive to climate (Johnson et al. 2011, Bell et al. 2014, Dobrowski et al. 2015), and thus we would expect that annual climate is critical in determining vegetation

responses to fire. Limited post-fire recruitment has been observed across parts of the western US (e.g. Savage and Mast 2005, Welch et al. 2016, Stevens-Rumann et al. 2018) suggesting that changes in climate may be limiting post-fire forest recovery, however, low recruitment density can result from a variety of interacting biotic and abiotic factors, and the pattern in itself does not necessarily indicate that climate conditions are too harsh for seedling recruitment. Assessing the extent to which climate conditions limit post-fire tree regeneration requires quantifying the relationship between post-fire recruitment and seasonal climate conditions during the year of germination. Furthermore, identifying areas that are most vulnerable to fire-catalyzed vegetation shifts requires not only identifying where climate is no longer suitable for post-fire regeneration, but also considering where high severity fires that kill existing mature forest are most likely to occur.

Managers charged with maintaining forest ecosystems and the services they provide are increasingly dealing with more area burned and fewer resources for post-fire management. Identifying where forests are likely to recover naturally, where a lack of seed sources may prevent recovery, and where climate may no longer be suitable for tree regeneration could inform decisions prioritizing post-fire management activities. A better understanding of vulnerability across the landscape to fire-catalyzed vegetation transitions could help inform planning efforts.

3. Materials and Methods

The majority of the results from this project were derived from one large field sampling effort, which combined with subsequent dendrochronological lab work, provided the data used in various analyses and manuscripts. The overall goal of this sampling effort was to reconstruct annual establishment patterns for *Pinus ponderosa* and *Pseudotsuga menziesii* following fire to identify annual climate conditions associated with successful post-fire regeneration. Below we describe this field sampling and lab work and then briefly describe the statistical analyses used in each manuscript to achieve specific objectives.

This JFSP project focused on the northern Rockies, but we combined efforts with an existing NSF grant (BCS-1461576; PI Solomon Dobrowski) and applied the same methods across regions. Fires in dry mixed-conifer forests dominated by *Pinus ponderosa* and/or *Pseudotsuga menziesii* were chosen across the western US in four broad regions: the Northern Rockies (NR), Colorado Front Range (CO), Southwest Mountains (SW), and Northern California (CA; Fig. 1). All fires burned between 1988 and 2007 to ensure sufficient time for post-fire recovery while excluding sites with trees that would be too large to destructively sample. Within each fire in the NR, SW, and CA, sampling areas were selected based on the following criteria: (1) sites had 30-year (1980-2009) mean climatic water deficits within the top 50th percentile (driest) for each species within each region, (2) sites burned at moderate to high severity based on the Monitoring Trends in Burn Severity (MTBS) dataset, (3) sites were within 1 km of a road, (4) sites had *P. ponderosa* and/or *P. menziesii* according to “Existing Vegetation” layers (from CALVEG for CA; from the US Forest Service for all other regions), and (5) sites had either northerly (315-45°) or southerly (135-225°) aspects. We excluded areas that had post-fire management based on the FACTS database, geospatial data from individual forests, field observations, and conversations with local silviculturalists. Using a GIS, two to 12 sampling points were randomly

placed within these sampling areas (depending on sampling area size). Because we were targeting sites with regeneration, sampling points that were farther than 100 m from a live seed source were excluded. Thus, our sampling was not intended to, nor does it, reflect the full range of post-fire regeneration after recent wildfires. The goal was to sample at least two sites per fire, but in the cases of some large fires, up to eight sites were sampled. In a few fires in the NR, only one site per fire was sampled. Selection of fires and sites from CO are described in more detail by Rother & Veblen (2017) but generally followed a similar sampling scheme. A total of 19 sites in CA, 10 in CO, 40 in NR, and 21 in SW were sampled (Table 1). The SW sites receive on average 54% of their annual precipitation between July and September, while this value declines to 32% for the CO sites, 13% for the NR sites and 3% for the CA sites.

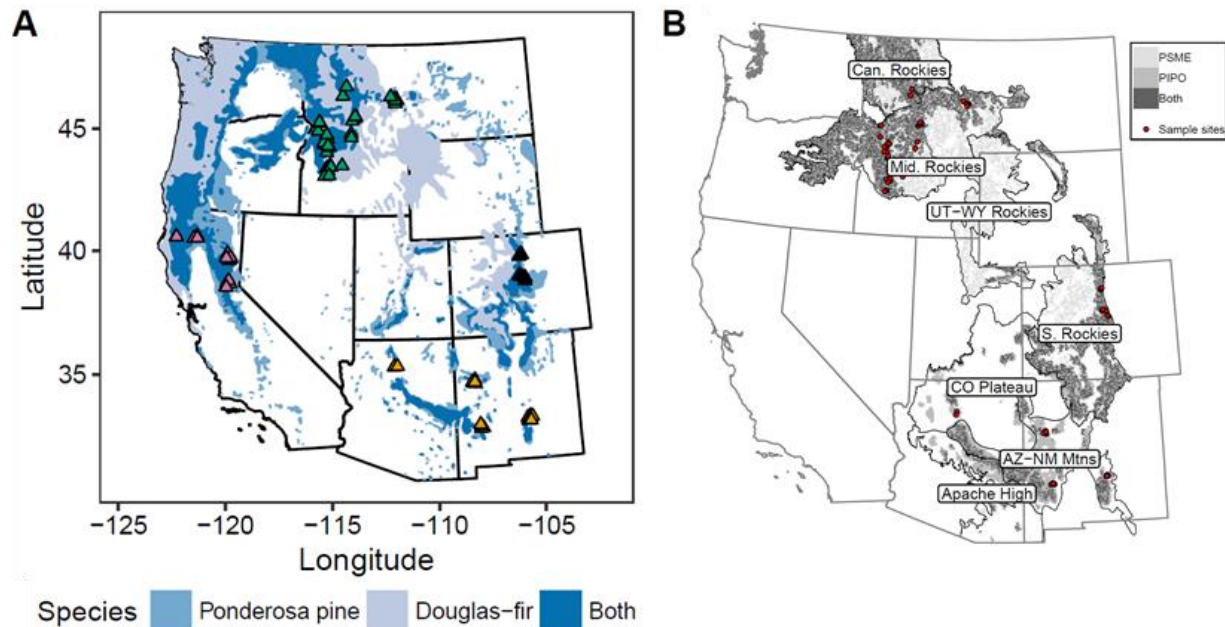


Figure 1. Study sites where field sampling was conducted in summer 2016 and 2017. All sites were used in the analysis for Davis et al. 2019 (A), while a subset of sites within the intermountain ecoregions were used for the analysis in Davis et al. 2020 (B). Shaded areas represent the range of ponderosa pine and Douglas-fir across the western US (A) and within the intermountain ecoregions (B).

In NR, SW, and CA sampling occurred in 60-m long belt transects with variable width (2-40 m) with the goal of destructively sampling about 30 seedlings or saplings (hereafter juveniles) per transect. All post-fire juveniles of the target species within the transects were destructively sampled. If no seedlings were present, site data was recorded and the zero density was retained in the dataset. Where none of the random sample points within a fire yielded high enough densities, plots were relocated to areas with regeneration. To destructively sample juveniles, soil was excavated and a segment of the stem from at least 10 cm below and 10 cm above the root-shoot boundary was removed. At three points along each transect, shrub cover was estimated in 2x3 m plots. Distance to the nearest seed source (live reproductive tree) of each species was recorded from the center of the plot with a laser range finder. Other site data such as canopy cover and live and dead tree basal area was also collected. Data collection in CO followed similar protocols (Rother and Veblen 2017).

To identify the germination year of the juveniles with annual precision, all tree samples were cut into 2.5 cm segments and each segment was progressively sanded with finer grit sandpaper (up to 600-1500 grit; Speer 2010). Each segment was aged under a 10-40x Nikon SMZ stereomicroscope and the oldest segment, which also corresponded with the first appearance of pith, was used as the age of that sample (Telewski 1993, League and Veblen 2006, Rother and Veblen 2017). We recorded visual marker years, but the young age of the trees precluded more formal cross-dating. To test the precision of our aging methods, 555 random samples were recounted by all three technicians responsible for aging trees. The mean (sd) difference in ring-count based ages among the three technicians was 0.298 (0.461) years. If ring boundaries were indistinct or pith dates were otherwise ambiguous the sample was not included in the final dataset, resulting in a combined total of 2820 aged juveniles (Table 1).

Table 1. Number of sites and trees sampled in each region, 30-year (1980-2009) mean annual climatic water deficit for those sites, and annual recruitment rate used as a threshold in each region for modeling a binomial response. Thresholds are the 25th or 50th percentile of annual recruitment rate for each species in each region for years in which at least one seedling established. Some sites had both species. PIPO is ponderosa pine and PSME is Douglas-fir.

Region	Species	Sites	Juveniles	Mean annual deficit (mm)	25 th percentile threshold (trees ha ⁻¹ yr ⁻¹)
CA	PIPO	13	320	741	17
	PSME	16	320	851	17
	total	19	640	800	16
CO	PIPO	10	355	603	
	PSME	0	0	-	
	total	10	355	603	42
NR	PIPO	32	658	572	
	PSME	29	670	538	56
	total	40	1328	554	13
SW	PIPO	16	297	835	
	PSME	18	200	768	12
	total	21	497	807	
All	PIPO	71	1630	-	-
	PSME	63	1190	-	-
	total	90	2820	-	-

Similar statistical analyses were used in two manuscripts produced by this project (Davis et al. 2019, Davis et al. 2020). The aim of the first (Davis et al. 2019) was to identify the relationship between seasonal climate and post-fire ponderosa pine and Douglas-fir recruitment at our study sites (Fig. 1A) using precise high resolution climate data (250 m) and plant-relevant variables (soil moisture and skin temperature) derived from an ecohydrological model (Maneta and

Silverman 2013). The aim of the second was to use similar models but with coarser climate data (4-km Terraclimate; Abatzoglou et al. 2018) to project climate suitability for post-fire regeneration across the range of these two species in the interior western US and identify areas that are vulnerable to fire-catalyzed vegetation transitions. In both studies, to model the relationship between annual recruitment and bioclimatic conditions at each site, we used boosted regression trees (BRT) (Elith et al. 2008) to construct separate BRT models for each species. Recruitment was modeled as a binomial response, with “success” representing when annual recruitment ($\#$ juveniles $\text{ha}^{-1} \text{yr}^{-1}$) exceeded a region-specific seedling density threshold. This threshold accounts for varying forest densities among regions and is defined as the 25th percentile of annual recruitment rates from among all years with recruitment for a given species in a given region (Table 1). The bioclimatic predictors in the models included static variables that remained the same over time: distance to seed source (measured in the field) and fire severity (dNBR; MTBS), and dynamic variables that varied with each year: time since fire and seasonal climate conditions. More details on the specific climate predictors and model selection can be found in Davis et al. 2019 and 2020.

We used the final models for each species for two purposes. First, we used the models from Davis et al. (2019) to project the probability of post-fire recruitment across all study sites from 1981-2015 using the climate time series from each site and a constant fire severity, distance to seed source, and time since fire. This allowed us to identify how climate suitability for post-fire recruitment had changed at these sites over time. Because these sites were limited to the warmer, drier edge of the range of ponderosa pine and Douglas-fir, we used the models from Davis et al. (2020) to create maps of recruitment probability across the range of ponderosa pine and Douglas-fir in the intermountain west (Fig. 1) from 1981-2019, as well as for ten years of a future climate scenario of +2°C (Qin et al. 2020). To calculate the proportion of each species’ range within the intermountain west vulnerable to fire-catalyzed change under current and future climate conditions, we overlaid the spatial grid predicting the likelihood of stand-replacing fire from Parks et al. (2018) with our predictions of post-fire recruitment probabilities. Together, this assessment highlights where there is a high likelihood of stand-replacing fire, if a fire were to occur, followed by a low likelihood of post-fire recruitment.

4. Results and Discussion

4.1 Post-fire regeneration and annual climate variability

Annual rates of post-fire ponderosa pine and Douglas-fir regeneration had strongly non-linear relationships with annual climate conditions, with distinct threshold responses to summer vapor pressure deficit (VPD), soil moisture, and maximum surface temperatures (Figs. 2 & 3; Davis et al. 2019). Seasonal to annual climate conditions from the early 1990’s through 2015 have crossed these climate thresholds at the majority of study sites, indicating conditions that are increasingly unsuitable for tree regeneration, particularly for ponderosa pine.

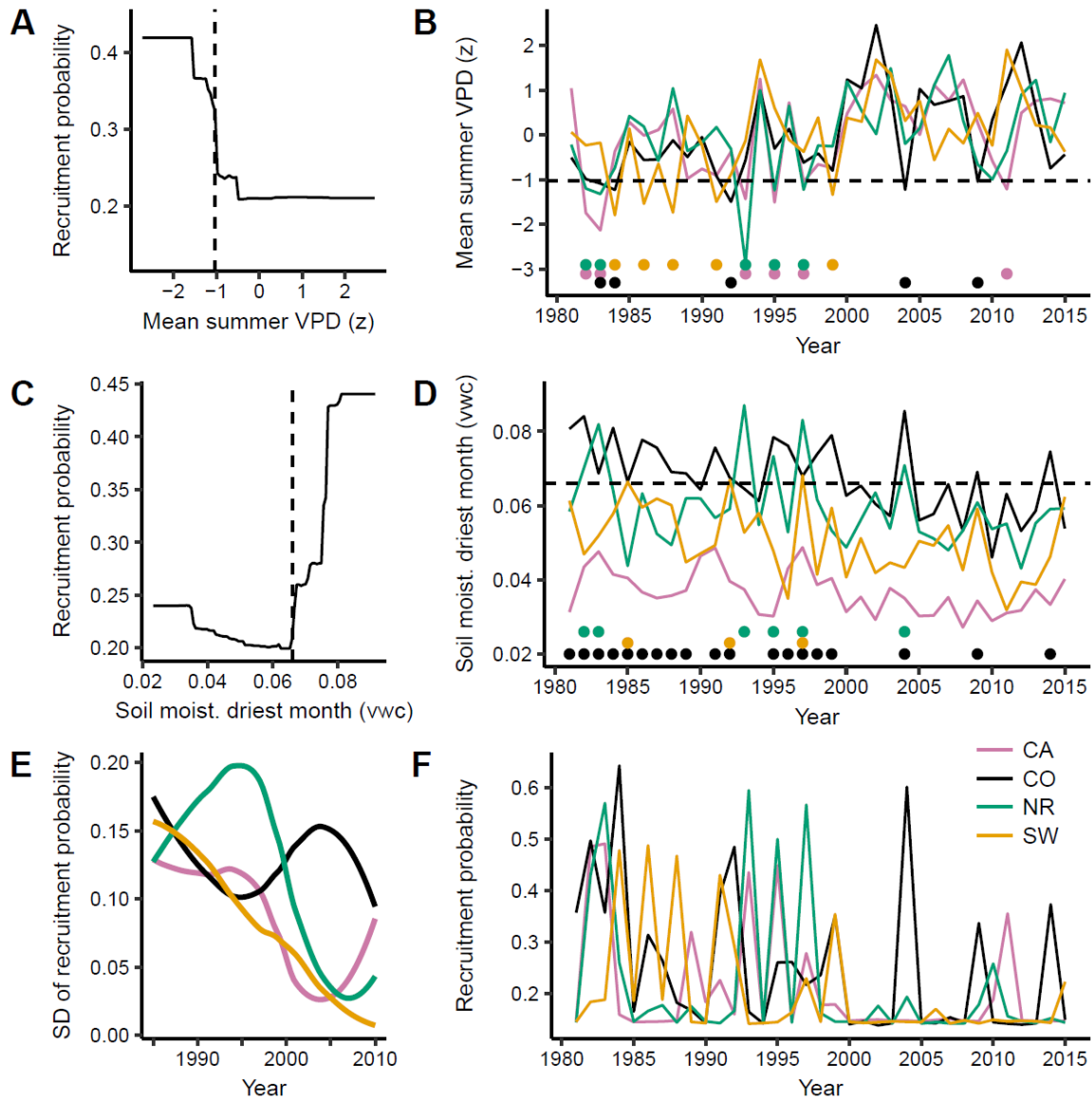


Figure 2. Threshold response of recruitment to annual climate and modeled annual recruitment probability for ponderosa pine. Partial dependency plots from a boosted regression tree model, show the marginal effect of the two most important climate variables on annual recruitment probability, after accounting for the average effects of all other variables in the model (A & C). Annual time series of climate variables at each site averaged by region (B & D). Climate thresholds are identified with vertical (A & C) and horizontal (B & D) dashed lines. Dots below the lines in B & D represent years when that specific climate variable was suitable for regeneration. The influence of both climate variables on regeneration are summarized by the modeled annual recruitment probability (F), while holding constant time since fire (1 yr), distance to seed source (50 m), and fire severity (dNBR 412). Variability in annual recruitment probability (E) is shown as the standard deviation (SD) of recruitment probability values from (F), calculated in 10-year moving windows and plotted with a LOWESS (locally-weighted polynomial regression) smooth. The units “vwc” indicates volumetric water content (ratio of water volume to soil volume). Figure from Davis et al. (2019).

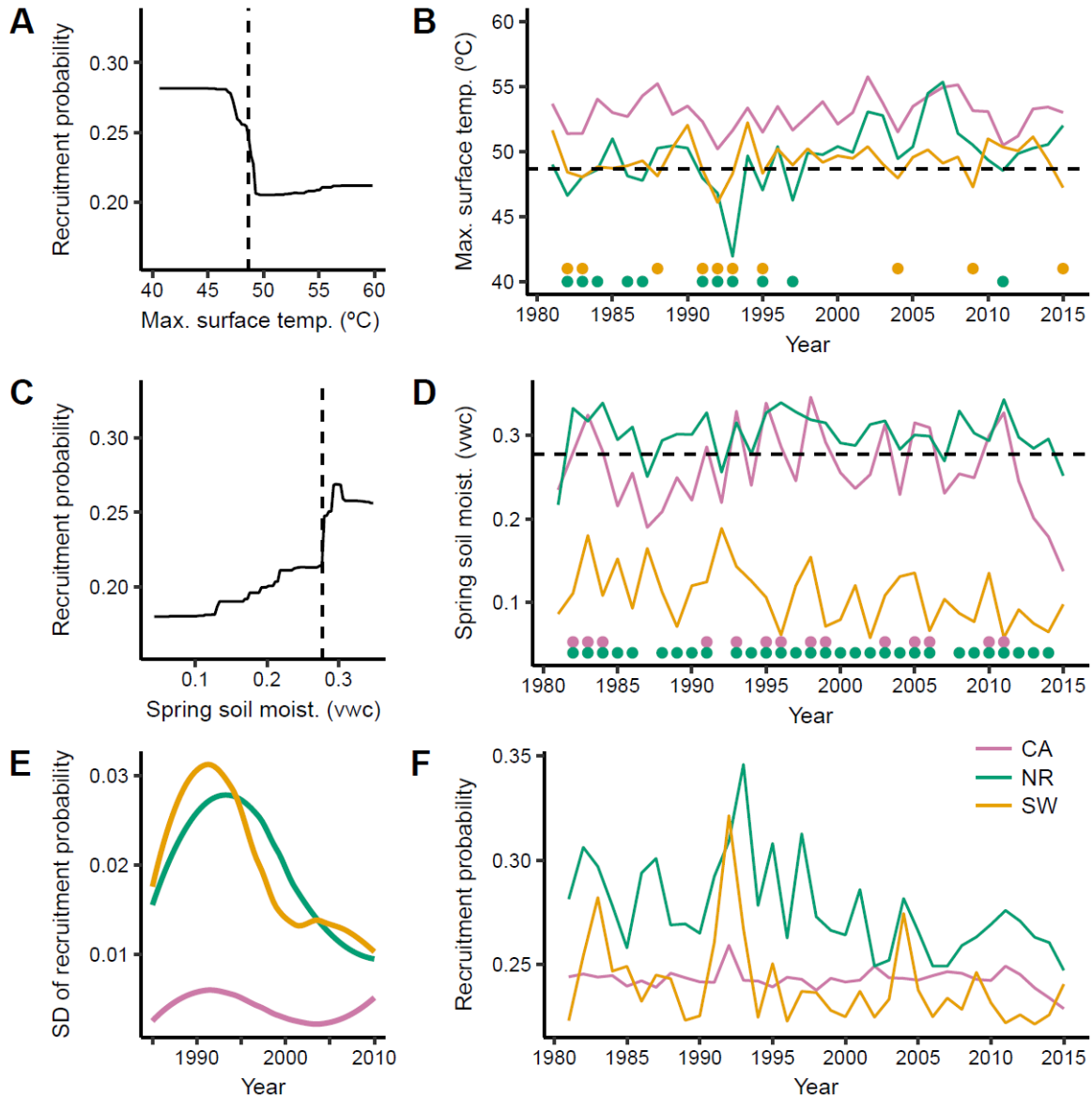


Figure 3. Threshold response of recruitment to annual climate and modeled annual recruitment probability for Douglas-fir. Partial dependency plots from a boosted regression tree model, show the marginal effect of the two most important climate variables on annual recruitment probability, after accounting for the average effects of all other variables in the model (A & C). Annual time series of climate variables at each site averaged by region (B & D). Climate thresholds are identified with vertical (A & C) and horizontal (B & D) dashed lines. Dots below the lines in B & D represent years when that specific climate variable was suitable for regeneration. The influence of both climate variables on regeneration are summarized by the modeled annual recruitment probability (F), while holding constant time since fire (1 yr), distance to seed source (50 m), and fire severity (dNBR 412). Variability in annual recruitment probability (E) is shown as the standard deviation (SD) of recruitment probability values from (F), calculated in 10-year moving windows and plotted with a LOWESS (locally-weighted polynomial regression) smooth. The units “vwc” indicates volumetric water content (ratio of water volume to soil volume). Figure from Davis et al. (2019).

Although annual climate was important, the nature of the fire event also strongly influenced the likelihood of post-fire regeneration. For example, the combined relative influence of annual climate variables on tree recruitment in our BRT models was 24% for ponderosa pine and 34% for Douglas-fir, while the relative influence of distance to seed source, which is largely determined by fire severity, was 32% for ponderosa pine and 21% for Douglas-fir (Figure 4; Davis et al. 2019). The probability of post-fire recruitment for both species declined with increasing distance to seed source and, for ponderosa pine, increasing fire severity.

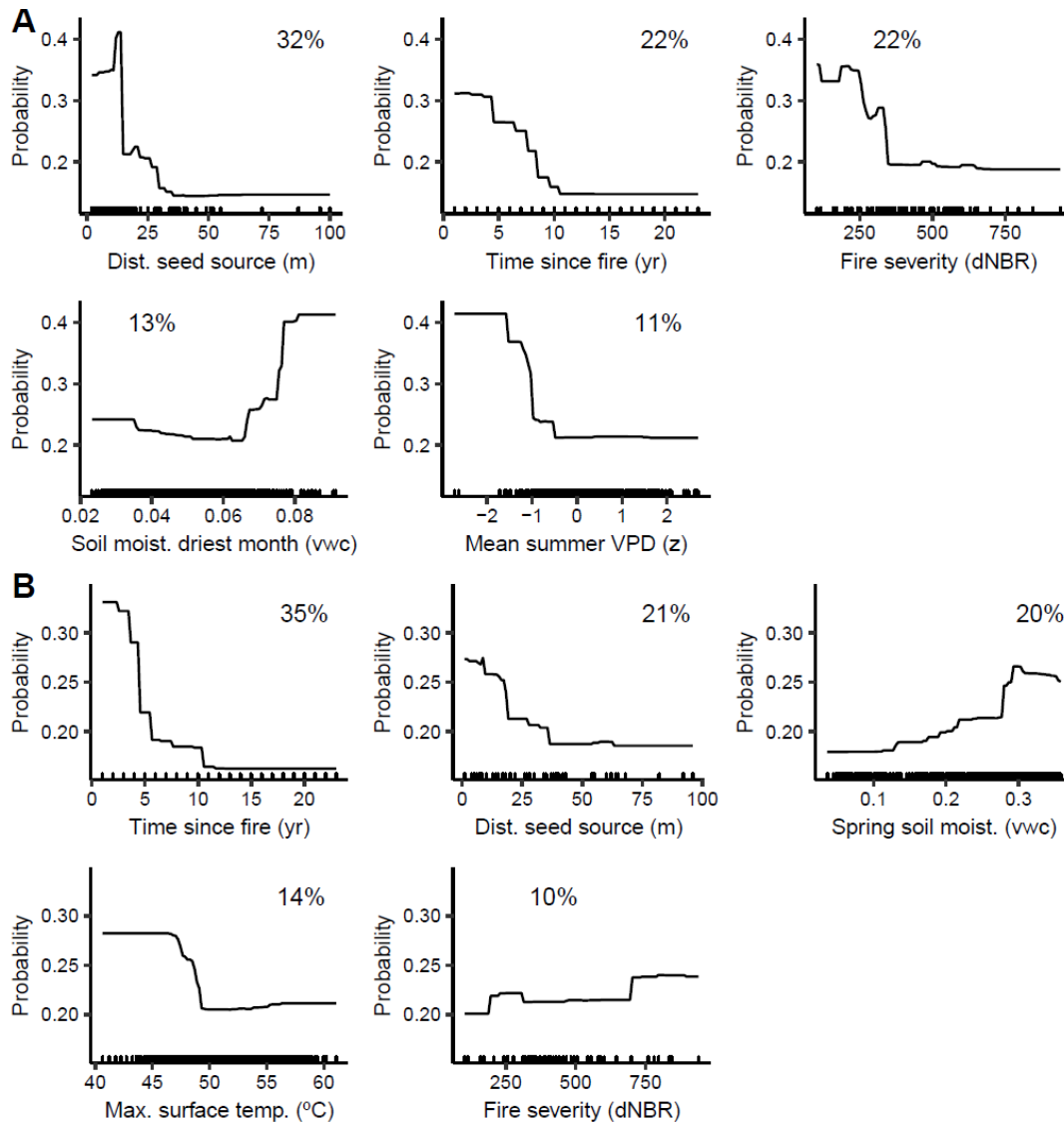


Figure 4. Partial dependency plots from final ponderosa pine (A) and Douglas-fir (B) boosted regression tree models showing the marginal effect of each variable on probability of crossing the recruitment threshold after accounting for the average effects of all other variables in the model. Percent values (%) on plots display the relative influence of that predictor. Vertical lines on x-axis (rug plot) show the distribution of observations in the dataset. The recruitment threshold in these models was the 25th percentile of recruitment density for years with recruitment for a given species in a given region (Table 1). Figure from Davis et al. (2019).

Our projections of climate suitability for post-fire recruitment across the range of ponderosa pine and Douglas-fir within the intermountain west also highlight how climate suitability has declined since the 1980s and projects further declines under a future climate scenario (Figs. 5 & 6; Davis et al. 2020). Across all ecoregions, 21% and 15% of the range of ponderosa pine and Douglas-fir, respectively, had climate conditions unsuitable for recruitment in the 1980s. These values increased to 32% and 20% in the 2000s, and 61% and 34% under the +2°C future climate scenario for ponderosa pine and Douglas-fir, respectively. Southern ecoregions had considerably lower climate suitability for both species, however under the future climate scenario there was a large decline in area with suitable climate for post-fire recruitment in the northern Rockies.

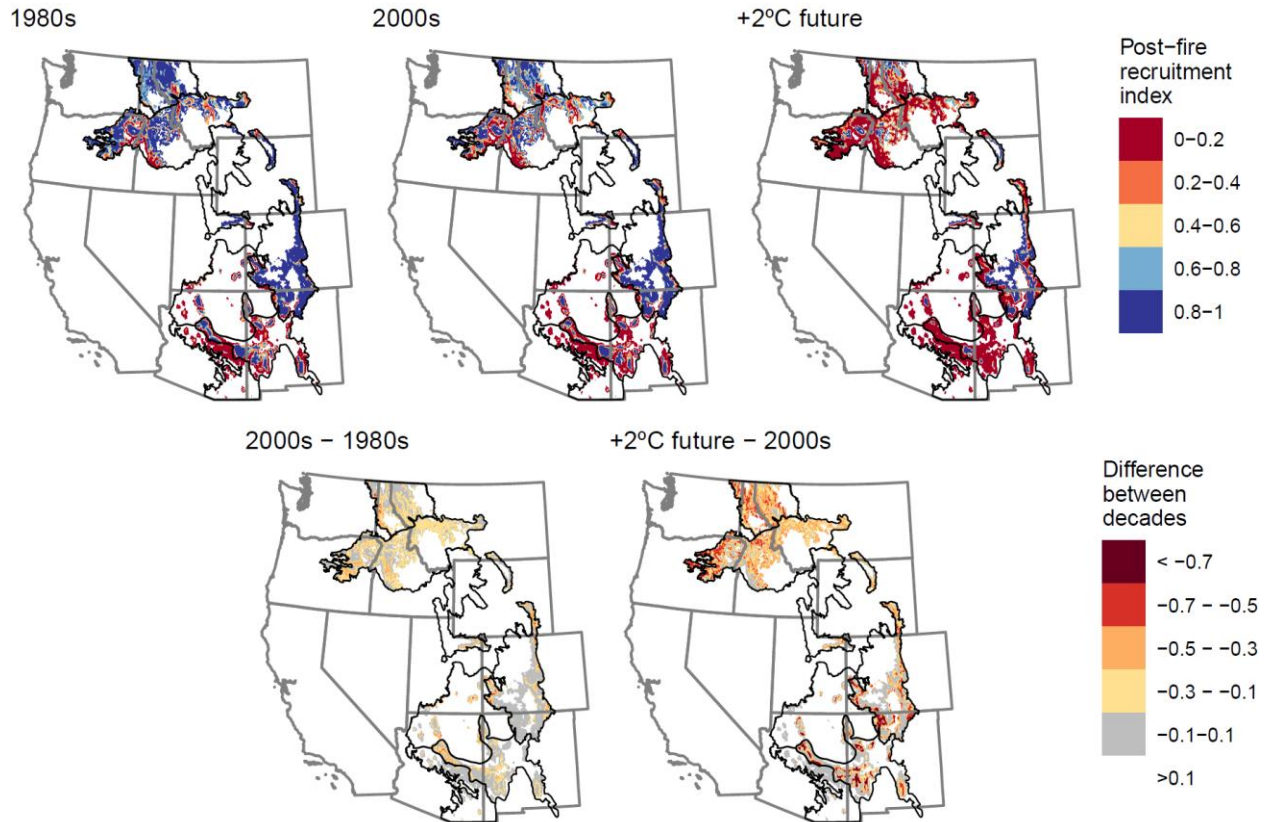


Figure 5. Maps of the projected post-fire recruitment index (proportion of first five post-fire years with climate suitable for regeneration) for ponderosa pine under recent climate conditions and the +2°C future scenario (upper row) and the difference in post-fire recruitment index between decades (lower row). The post-fire recruitment index is averaged for each decade shown. Projections are clipped to the range of ponderosa pine (Ellenwood et al. 2015) and the intermountain ecoregions (black outline; Fig. 1B). Figure from Davis et al. (2020).

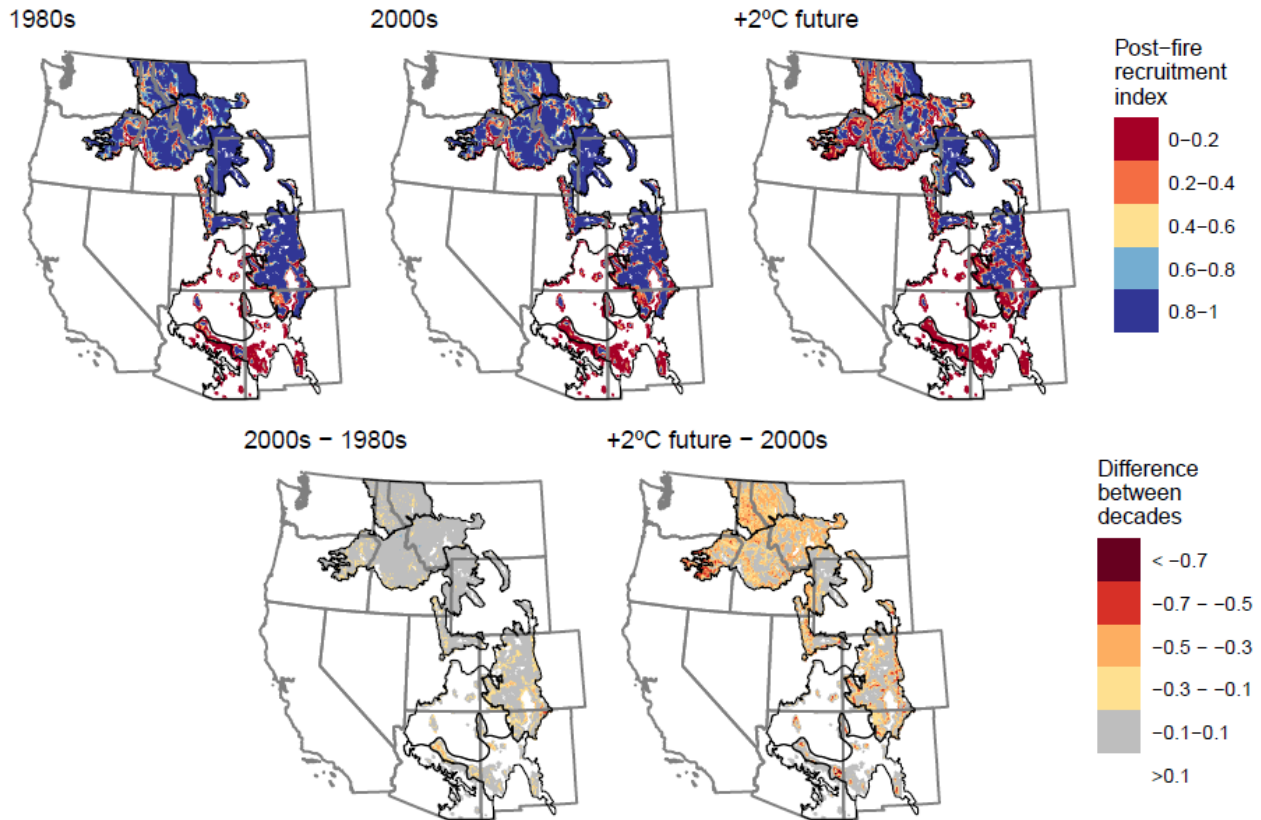


Figure 6. Maps of the projected post-fire recruitment index (proportion of first five post-fire years with climate suitable for regeneration) for Douglas-fir under recent climate conditions and the +2°C future scenario (upper row) and the difference in post-fire recruitment index between decades (lower row). The post-fire recruitment index is averaged for each decade shown. Projections are clipped to the range of Douglas-fir (Ellenwood et al. 2015) and the intermountain ecoregions (black outline; Fig. 1B). Figure from Davis et al. (2020).

4.2 Vulnerability to fire-catalyzed vegetation shifts

Vulnerability to fire-catalyzed vegetation shifts also increased over time. Across the study region, 6% and 4% of the area was vulnerable to fire-catalyzed shifts in the 1980s, for ponderosa pine and Douglas-fir, respectively. These numbers increased to 16% (ponderosa pine) and 10% (Douglas-fir) under future climate conditions (Davis et al. 2020). The area vulnerable to fire-catalyzed shifts under future climate conditions was lowest in the three northernmost ecoregions where it ranged from 1-10%. While 14-62% of the area in these northern ecoregions exhibited climate conditions unsuitable for post-fire recruitment under future climate conditions, these areas also tended to be more likely to burn at lower severity. Within each ecoregion, the lowest elevation areas within each species' distribution tended to have the lowest climate suitability for recruitment, but due to an elevational trend in the probability of stand-replacing fire, vulnerability to fire-catalyzed vegetation shifts tended to peak at intermediate elevations.

Overall, our results provide a mechanism linking recent observations of reduced post-fire conifer regeneration (e.g. Roccaforte et al. 2012, Welch et al. 2016, Stevens-Rumann et al. 2018) to changes in post-fire climate conditions. They highlight that climate change has likely already had an impact on post-fire conifer regeneration and that ongoing changes in climate will likely

further limit post-fire ponderosa pine and Douglas-fir regeneration in the upcoming decades, especially at sites near the margins of these two species ranges (e.g. low elevations and southern ecoregions). These results agree with a growing consensus that climate change will significantly affect forest recovery, even in dry mixed conifer forests with fire-adapted species (Kemp et al. 2019) and highlight the potential for wildfire to catalyze conversions of forests to non-forest ecosystems (Coop et al. 2020). Our results also highlight the importance of seed availability to post-fire recovery, in agreement with other recent work (e.g. Kemp et al. 2016, Stevens-Rumann et al. 2018, Coop et al. 2019, Downing et al. 2019), which suggests that efforts to reduce fire severity and increase living seed sources on the landscape following fire can significantly increase the likelihood of post-fire regeneration.

Table 2. Percentage of the range of ponderosa pine or Douglas-fir (Ellenwood et al. 2015) within each ecoregion (Fig. 1B) that is vulnerable to fire-catalyzed vegetation shifts, defined as areas with (a) a post-fire recruitment index < 0.2, and (b) predicted to have stand-replacing fire, if a fire were to occur. The post-fire recruitment index is the proportion of the first five post-fire years with climate suitable for regeneration (i.e. an index of 0.2 signifies that one of the first five post-fire years had suitable climate). “Mtns” is “mountains.” Table from Davis et al. (2020).

Ecoregion	Ponderosa pine			Douglas-fir		
	1980s	2000s	+2°C future	1980s	2000s	+2°C future
All	6	9	16	4	6	10
Canadian Rocky Mtns	0	0	7	0	0	1
Middle Rockies - Blue Mtns	1	2	10	0	0	3
Utah-Wyoming Rocky Mtns	0	0	0	1	2	6
Southern Rocky Mtns	3	6	15	4	7	13
Colorado Plateau	27	42	54	42	51	62
Arizona-New Mexico Mtns	5	7	13	11	14	20
Apache Highlands	51	55	59	61	63	63

4.3 Additional Research Results

The project also produced additional results related to, but not directly addressing, the project’s original objectives. Below are the abstracts from four additional manuscripts that were produced with support from this grant.

Littlefield CE, Dobrowski SZ, Abatzoglou JT, Parks SA, and Davis KT. (2020) A climatic dipole drives short- and long-term patterns of postfire forest recovery in the western United States. *Proceedings of the National Academy of Sciences*. 117:29730-29737. <https://doi.org/10.1073/pnas.2007434117>

Researchers are increasingly examining patterns and drivers of postfire forest recovery amid growing concern that climate change and intensifying fires will trigger ecosystem transformations. Diminished seed availability and postfire drought have emerged as key constraints on conifer recruitment. However, the spatial and temporal extent to which recurring modes of climatic variability shape patterns of postfire recovery remain largely unexplored. Here, we identify a north–south dipole in annual climatic moisture deficit anomalies across the Interior West of the US and characterize its influence on forest recovery from fire. We use annually resolved establishment models from

dendrochronological records to correlate this climatic dipole with short-term postfire juvenile recruitment. We also examine longer-term recovery trajectories using Forest Inventory and Analysis data from 989 burned plots. We show that annual postfire ponderosa pine recruitment probabilities in the northern Rocky Mountains (NR) and the southwestern US (SW) track the strength of the dipole, while declining overall due to increasing aridity. This indicates that divergent recovery trajectories may be triggered concurrently across large spatial scales: favorable conditions in the SW can correspond to drought in the NR that inhibits ponderosa pine establishment, and vice versa. The imprint of this climatic dipole is manifest for years postfire, as evidenced by dampened long-term likelihoods of juvenile ponderosa pine presence in areas that experienced postfire drought. These findings underscore the importance of climatic variability at multiple spatiotemporal scales in driving cross-regional patterns of forest recovery and have implications for understanding ecosystem transformations and species range dynamics under global change.

Davis KT, Dobrowski S, Holden Z, Higuera PE, and Abatzoglou JT. (2019) Microclimatic buffering in forests of the future: The role of local water balance. *Ecography*. 42:1-11. <https://doi.org/10.1111/ecog.03836>

Forest canopies buffer climate extremes and promote microclimates that may function as refugia for understory species under changing climate. However, the biophysical conditions that promote and maintain microclimatic buffering and its stability through time are largely unresolved. We posited that forest microclimatic buffering is sensitive to local water balance and canopy cover, and we measured this effect during the growing season across a climate gradient in forests of the northwestern United States (US). We found that forest canopies buffer extremes of maximum temperature and vapor pressure deficit (VPD), with biologically meaningful effect sizes. For example, during the growing season, maximum temperature and VPD under at least 50% forest canopy were 5.3°C and 1.1 kPa lower on average, respectively, compared to areas without canopy cover. Canopy buffering of temperature and vapor pressure deficit was greater at higher levels of canopy cover, and varied with water balance, implying that buffering effects are subject to changes in local hydrology. We project changes in the water balance for the mid-21st century and predict how such changes may impact the ability of western US forests to buffer climate extremes. Our results suggest that some forests will lose their capacity to buffer climate extremes as sites become increasingly water limited. Changes in water balance combined with accelerating canopy losses due to increases in the frequency and severity of disturbance will create potentially non-linear changes in the microclimate conditions of western US forests.

Hankin L, Higuera PE, Davis KT, and Dobrowski SZ. (2019) Impacts of growing-season climate on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir forests. *Ecosphere*. 10:e02679. <https://doi.org/10.1002/ecs2.2679>

We studied the impacts of climate variability on low-elevation forests in the U.S. northern Rocky Mountains by quantifying how post-fire tree regeneration and radial growth varied with growing season climate. We reconstructed post-fire regeneration and radial growth rates of *Pinus ponderosa* and *Pseudotsuga menziesii* at 33 sites that burned between 1992 and 2007, by aging seedlings at the root–shoot boundary. We also measured radial growth in adult trees from 12 additional sites that burned between 1900 and 1990. To quantify the relationship between climate and regeneration, we characterized seasonal climate before, during, and after recruitment pulses using superposed epoch analysis. To quantify growth sensitivity to climate, we performed moving regression analysis for each species and for juvenile and adult life stages. Climatic conditions favoring regeneration and tree growth differed between species. Water deficit and temperature were significantly lower than average during recruitment pulses of ponderosa pine, suggesting that germination-year climate limits regeneration. Growing degree days were significantly higher than average during years with Douglas-fir recruitment pulses, but water deficit was significantly lower one year following pulses, suggesting moisture sensitivity in two-year-old seedlings. Growth was also sensitive to water deficit, but effects varied between life stages, species, and through time, with juvenile ponderosa pine growth more sensitive to climate than adult growth and juvenile Douglas-fir growth. Increasing water deficit corresponded with reduced adult growth of both species. Increases in maximum temperature and water deficit corresponded with increases in juvenile growth of both species in the early 20th century but strong reductions in growth for juvenile ponderosa pine in recent decades. Changing sensitivity of growth to climate suggests that increased temperature and water deficit may be pushing these species toward the edge of their climatic tolerances. Our study demonstrates

increased vulnerability of dry mixed-conifer forests to post-fire regeneration failures and decreased growth as temperatures and drought increase. Shifts toward unfavorable conditions for regeneration and juvenile growth may alter the composition and resilience of low-elevation forests to future climate and fire activity.

Davis KT, Higuera, PE, and Sala A. (2018). A framework for anticipating fire-mediated impacts of climate change. *Functional Ecology*. 32:1729-1745. <https://doi.org/10.1111/1365-2435.13132>

Climate change indirectly affects forest ecosystems through changes in the frequency, size, and/or severity of wildfires. In addition to its direct effects prior to fire, climate also influences immediate postfire recruitment, with consequences for future vegetation structure and fire activity. A major uncertainty, therefore, is if, when and where vegetation shifts will occur. With an emphasis on species traits, we use a demographic framework to examine how the interaction of changing climate and fire will affect postfire woody vegetation recruitment and the likelihood of vegetation shifts. Each demographic stage – adult mortality, propagule availability, seed germination, seedling establishment, and seedling survival – serves as a filter through which a species must pass for establishment and recovery to occur. We apply this framework to case studies in western North American forests, including boreal and southwestern U.S. *Pinus ponderosa* forests, to help understand the mechanisms behind recent postfire vegetation changes. The case studies highlight how changes in climate and fire properties will make it increasingly difficult for some species to pass through each demographic filter in the future. As climate warming continues, we expect increased dominance of species that resprout following fire, maintain canopy or soil seed banks, have long distance seed dispersal, produce drought-tolerant seedlings, and/or reach reproductive maturity quickly. The persistence of postfire vegetation shifts will depend on the ratio of recovery time to disturbance interval(s). An advantage of the demographic-filter framework is that it places emphasis on mechanisms, thus improving our ability to anticipate future vegetation shifts. As such, it highlights the clear need for more mechanistic studies of postfire recruitment to disentangle the relative effects of multiple drivers in postfire environments.

Hankin L, Higuera PE, Davis KT, and Dobrowski SZ. (2018) Accuracy of node counts for aging two dominant conifers in western North America. *Forest Ecology and Management*. 427: 365-371. <https://doi.org/10.1016/j.foreco.2018.06.001>

Accurately aging trees is critical for understanding tree demography and tree responses to environmental change. Given the proliferation of studies aimed at understanding the effects of climate and disturbance on forest ecosystems, it is important to understand the tradeoffs between field-based age estimates and precise dendrochronological techniques. We assessed the accuracy of age estimates from node counts in the field against precise tree-ring counts at the root-shoot boundary, in 1279 ponderosa pine and 1268 Douglas-fir seedlings sampled from across three study regions in the western U.S. We also assessed the accuracy of age estimates from bud-scar counts in the field against node counts and precise tree-ring counts in a subset of 757 seedlings from the Northern Rockies. Node counts systematically underestimated ring counts by an average of 4.1 years, with bias increasing with tree age. At annual, ± 1 -, ± 2 -, and ± 5 -yr precision, the accuracy of node counts was 5%, 15%, 29%, and 74% across all regions and species, respectively. Similar results were found for bud scars. Given the magnitude of the bias between field-based methods and ring counts, it is critical to select appropriate aging methods, based on the precision required to answer specific ecological questions. To improve the accuracy of field-based age estimates in these species, we provide a tool for correcting for the bias when precise dendrochronological aging is not feasible.

4.4 Dissemination of Research Results

Science delivery activities involved significant collaboration with the Northern Rockies Fire Science Network (NRFSN) and included two publications (one [research brief](#) and one [science review](#)), a [webinar](#), and a presentation at a NRFSN [workshop](#). Additional outreach beyond collaboration with NRFSN included a [webinar](#) hosted by the North Central Climate Adaptation Science Center, presentations at multiple workshops held by the US Forest Service for reforestation specialists from Regions 1-4, interviews with local and international media outlets

([BBC](#) (minute 8:10); [MTPR](#); [CNN](#); [Inside Climate News](#); [Reuters](#)), and presentations at scientific conferences (International Fire Ecology and Management Congress, Ecological Society of America Annual Meetings, North American Forest Ecology Workshop). We also created an interactive version of the results from Davis et al. 2020 that is available [here](#).

Models developed through this project are being used in the [RegenMapper](#) tool that is being developed in collaboration with the US Forest Service Region 1 to provide spatial predictions of the probability of ponderosa pine and Douglas-fir regeneration within recent fire boundaries to help inform post-fire management actions such as reforestation.

5. Conclusions and Implications for Management and Future Research

Our results highlight the potential for the combined influences of climate warming and an increase in wildfire activity to substantially impact forest ecosystems through fire-catalyzed vegetation shifts. The warmest sites in our study have already crossed climate thresholds for post-fire ponderosa pine and Douglas-fir recruitment, and we expect limited tree regeneration at these and similar sites. When predicting across the range of ponderosa pine and Douglas-fir forests in the US intermountain west, we found significant portions of these forests are vulnerable to fire-catalyzed vegetation shifts, and this vulnerability is projected to increase in upcoming decades as fires continue to burn more area under warmer, drier climate conditions (Abatzoglou and Williams 2016, Littell et al. 2018). Given that regeneration of other tree species is also limited by warm, dry conditions (e.g., Conlisk et al. 2017, Andrus et al. 2018), fire-catalyzed vegetation shifts may also become more prevalent in other forest types (Coop et al. 2020).

Our research also highlights the significant changes in microclimate that can occur due to loss of canopy cover and other changes to vegetation and soil following fire. The magnitude of the differences in maximum temperature and VPD that we observed in forested or unburned areas compared to unforested or recently burned areas suggests that changes in microclimate due to fire could be significant enough to push sites across climate thresholds for post-fire recruitment.

Our results have direct implications for management strategies aimed at maintaining ponderosa pine and Douglas-fir forests in the US intermountain west. For example, within most regions, particularly in the northern ecoregions, we expect that some areas will retain climate suitable for post-fire regeneration of these two species, even under the +2°C future climate scenario. In these areas with suitable climate but where a seed source is lacking, post-fire management can focus on reforestation. The RegenMapper tool that we are helping inform based on the models developed in this project will help to identify these areas on specific burned landscapes to help managers prioritize reforestation efforts. Future research could work to incorporate the changes to microclimate that we expect based on loss of canopy cover and the biophysical context of the site.

In areas where climate is marginal for post-fire regeneration, managers conducting post-fire planting to maintain ponderosa pine and Douglas-fir on the landscape may consider implementing assisted gene flow (Aitken and Whitlock 2013) by planting seeds from warmer and drier sites in what are currently considered cool, moist sites (Rehfeldt et al. 2014). There is some evidence that assisted gene flow may improve growth and survival, however many uncertainties remain regarding the potential effectiveness of this strategy (Kolb et al. 2019, Young et al. 2020). Additionally, managers may face policy constraints that limit the use of this

strategy. More research is needed to better understand the potential risks and benefits of this strategy, especially over longer time periods, and to help refine seed zones to better align with future climate conditions and provide more guidance to managers on the ground. Other strategies to help promote seedling survival in sites with marginal climate, such as drought conditioning or microsite planting, are being studied in southern ecoregions where post-fire tree planting success can be low (Kolb et al. 2019, Sloan et al. 2020).

Finally, in areas where climate is unsuitable for regeneration, managers may emphasize pre-fire efforts to limit the occurrence of high severity fire and/or the size of stand-replacing patches, prioritizing areas where maintaining forest cover is especially important (e.g. municipal watersheds, old-growth forest). For example, fuel treatments that include thinning and prescribed fire have generally been found to decrease fire severity (e.g. Prichard and Kennedy 2014, Prichard et al. 2020) and thus have the potential to promote both higher survival of mature trees and increased post-fire regeneration (Stevens et al. 2014). Additionally, maintaining some canopy cover on sites will help ameliorate harsh microclimate conditions near the ground where tree seedlings are regenerating. Nevertheless, given the long-standing prevalence of stand-replacing fire in many western forests (Pierce et al. 2004) and current trends on increasing fire severity (Parks and Abatzoglou 2020), stand-replacing fire is inevitable in at least some sites with climate unsuitable for regeneration. In these areas, maintenance of ponderosa pine and Douglas-fir will be challenging, if not impossible. Improved predictions of future fire risk would help to better identify these areas on the landscape. In areas with high risk of high-severity fire and low likelihood of post-fire regeneration, managers may need to weigh the acceptability of a vegetation transition versus the high mitigation costs that come with managing for resilience (Higuera et al. 2019). For example, in the southwestern US, survival of ponderosa pine seedlings planted post-fire averaged only 25% after 5-8 years (Ouzts et al. 2015), suggesting that plantings may need to be repeated for several years to achieve desired success rates. Where high mitigation costs are untenable, but tree cover is desired to achieve management goals, managers may need to consider planting tree species that are adapted to warmer and drier conditions than ponderosa pine and Douglas-fir, especially in southern ecoregions and at low-elevation sites and southerly aspects. Researchers in the Southwest have already started experimenting with planting pine species adapted to warmer conditions (e.g. Hess and Fulé 2020). In other situations, it may make sense to accept or direct fire-driven vegetation shifts (McWethy et al. 2019), given that new vegetation types could be more resilient to future climate and fire conditions (Coop et al. 2016). Further research is needed to understand the implications of accepting vegetation transitions for ecosystem services, achieving management goals, and wildlife. Additionally, the effectiveness and long-term impacts of management strategies aimed at directing post-fire vegetation shifts are poorly understood and could be the topic of future research.

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Appendix B: List of Completed Scientific/Technical Publications/Science Delivery Products

Articles in peer-reviewed journals, with project supported personnel in bold

- Coop JD, Parks SA, Stevens-Rumann CS, Crausbay S, **Higuera PE**, Hurteau MD, Tepley A, Whitman E, Assal T, Collins BM, **Davis KT**, **Dobrowski S**, Falk DA, Fornwalt PJ, Fulé PZ, Harvey BJ, Kane VR, Littlefield CE, Margolis EQ, North M, Parisien MA, Prichard S, and Rodman KC. (2020) Wildfire-driven forest conversion in western North American landscapes. *Bioscience*, biaa061.
- Davis KT**, **Dobrowski SZ**, **Higuera PE**, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, and Maneta MP. (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *PNAS*. 116:6193-6198.
Selected press coverage: [BBC](#) (minute 8:10); [MTPR](#); [CNN](#); [Inside Climate News](#)
[Highlighted in "News and Views" section of Nature Plants, by Keeley, van Mantgem, and Falk.](#)
- Davis KT**, **Dobrowski S**, Holden Z, **Higuera PE**, and Abatzoglou JT. (2019) Microclimatic buffering in forests of the future: The role of local water balance. *Ecography*. 42:1-11. *Editor's choice*. Video abstract: <https://youtu.be/wvlKxvK6F2M>
- Davis KT**, **Higuera PE**, **Dobrowski SZ**, Parks SA, Abatzoglou JT, Rother MT, and Veblen TT. (2020) Fire-catalyzed vegetation shifts in ponderosa pine and Douglas-fir forests of the western United States. *Environmental Research Letters*. 15:1040b8. Selected press coverage: [Reuters](#) Interactive results: https://kt-davis.shinyapps.io/fire_catalyzed_change/
- Davis KT**, **Higuera PE**, and Sala A. (2018). A framework for anticipating fire-mediated impacts of climate change. *Functional Ecology*. 32:1729-1745.
- Hankin L**, **Higuera PE**, **Davis KT**, and **Dobrowski SZ**. (2019) Impacts of growing-season climate on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir forests. *Ecosphere*. 10:e02679.
- Hankin L**, **Higuera PE**, **Davis KT**, and **Dobrowski SZ**. (2018) Accuracy of node counts for aging two dominant conifers in western North America. *Forest Ecology and Management*. 427: 365-371.
- Littlefield CE, **Dobrowski SZ**, Abatzoglou JT, Parks SA, and **Davis KT**. (2020) A climatic dipole drives short- and long-term patterns of postfire forest recovery in the western United States. *Proceedings of the National Academy of Sciences*. 117:29730-29737.
- Wolf KD, **Higuera PE**, **Davis KT**, **Dobrowski SZ** (In Press, as of January 2021) Wildfire impacts on forest microclimate vary with biophysical context. *Ecosphere*.

Technical reports

- Davis KT** and **Hankin LE**. (2020) Climatic Controls on Post-fire Ponderosa Pine and Douglas-fir Regeneration and Growth. Northern Rockies Fire Science Network Research Brief No. 8.
- Stevens-Rumann C, Morgan P, **Davis KT**, Kemp K, and Blades J. (2020) Post-fire tree regeneration (or lack thereof) can change ecosystems. Northern Rockies Fire Science Network Science Review No. 4.

Text books or book chapters

Hood SM, Harvey BJ, Fornwalt PJ, Naficy CE, Hansen WD, **Davis KT**, Battaglia MA, Stevens-Rumann C, and Saab V. (In Press) Fire Ecology of Rocky Mountain Forests. *In Past, Present, and Future Fire Ecology and Management across US Forested Ecosystems*. Ed. Collins B. & Greenberg CH. Springer Nature.

Graduate thesis

Hankin, L. E. (2018) Annual climate impacts on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir in the northern Rocky Mountains. MS Thesis, Systems Ecology. University of Montana ScholarWorks. <https://scholarworks.umt.edu/etd/11192>

Website development

Models developed through this project inform the projections of post-fire recruitment probability on this website which is a tool in development by collaborator Zack Holden (USFS Region 1) to help managers plan post-fire reforestation efforts: <https://orthanc.dbs.umt.edu/regenmapper/>

We also developed a web application to interactively view the results from Davis et al. 2020 which can be found here: https://kt-davis.shinyapps.io/fire_catalyzed_change/

Presentations/webinars/other outreach/science delivery materials

Davis KT, Higuera PE, Dobrowski SZ, Parks SA, Abatzoglou JT (2020) Increasing risk of fire-catalyzed change in ponderosa pine and Douglas-fir forests. *The Ecological Society of America Annual Meeting*.

Davis, KT. (2020) Post-fire conifer regeneration in a changing climate. North Central Climate Adaptation Science Center Webinar Series. July 9, 2020. <https://youtu.be/RbksCunuB0>

Davis, KT. (2020) Assessing the importance of seasonal climate, microclimate, and fire severity for post-fire ponderosa pine and Douglas-fir regeneration. USFS R1-R4 Reforestation – Stand Improvement Workshop, Northern Rockies Training Center, Missoula, MT.

Davis, KT (2019) Managing forests for climate and community benefits. Invited panel member. Natural Climate Solutions Symposium, The Nature Conservancy and UC Davis, Sacramento, CA.

Davis, KT (2019) Post-fire climate limits ponderosa pine and Douglas-fir regeneration. Presentation at the Northern Rockies Fire Science Network workshop: Wilderness Fire Management: Easier Now or Later? Choteau, MT. Presentation available [here](#).

Davis, KT and Wolf, K (2019) Forests and fire in a changing climate. Public presentation at the North Valley Public Library, Stevensville, MT.

Davis, KT (2019) Climatic controls on post-fire regeneration and growth in ponderosa pine and Douglas-fir. Webinar hosted by the Northern Rockies Fire Science Network. <https://www.nrfirescience.org/event/climatic-controls-post-fire-regeneration-and-growth-ponderosa-pine-and-douglas-fir>

Davis KT. (2019) Effects of climate, fire severity, and biotic interactions on post-fire conifer regeneration in low elevation forests of the western U.S. University of Montana Systems Ecology Spring Seminar Series, January 10, 2019, Missoula, MT.

Davis KT, Higuera P, Dobrowski S, and Wolf K. (2019) Fuel treatments as a means for mitigating fire-catalyzed forest change. *8th International Fire Ecology and Management Congress*, Tucson, AZ.

- Davis KT, Higuera P, Dobrowski S, Holden Z, Veblen T, Rother M, and Parks S. (2019) Anticipating the effects of climate change and wildfire on low elevation forests in the western US. *North American Forest Ecology Workshop*, Flagstaff, AZ.
- Davis KT, Higuera P, Dobrowski S, Holden Z, Veblen T, Rother M, and Parks S. (2019) Low-elevation forests have crossed critical climate thresholds for post-fire tree recruitment. *US-International Association for Landscape Ecology Annual Meeting*, Fort Collins, CO.
- Davis KT, Dobrowski S, Holden Z, Higuera P, and Abatzoglou JT. (2018) Microclimatic buffering in forests of the future: The role of local water balance. *Mountain Climate Conference*, Gothic, CO.
- Davis KT, Higuera P, Dobrowski S, Holden Z, and Parks S. (2018) Climatic controls on post-fire conifer regeneration in low-elevation forests of the western U.S. *Fire Continuum Conference*, Missoula, MT.
- Davis KT, Higuera P, Dobrowski S, Holden Z, and Parks S. (2018) Climatic controls on post-fire conifer regeneration in low-elevation forests of the western U.S. USFS Missoula Fire Sciences Laboratory Seminar Series, February 1, 2018, Missoula, MT.
- Davis, KT (2018) Climatic controls on post-fire ponderosa pine regeneration in low-elevation forests of the western U.S.” USFS Region 1 Reforestation - TSI Workshop, Northern Rockies Training Center, Missoula, MT.
- Davis KT, Holden Z, Higuera P, and Dobrowski S. (2017) Canopy cover moderates seedling microclimate: implications for conifer regeneration under a changing climate. *The Ecological Society of America Annual Meeting*, Portland, OR.
- Hankin L, Higuera P, Davis KT, Dobrowski S, Parks S. (2017) Climate variability and post-fire forest regeneration in the Northern Rockies. *The Ecological Society of America Annual Meeting*, Portland, OR.
- Hankin, L. E., P. E. Higuera, K. T. Davis, and S. Z. Dobrowski. (2018) Climate Variability Impacts Growth and Post-Fire Tree Regeneration Differently among Juveniles and Adults of Ponderosa Pine and Douglas-fir. *The Fire Continuum Conference*, hosted by the International Association of Wildland Fire and the Association for Fire Ecology, Missoula, MT.
- Higuera, P. E., A. M. Young, and K. T. Davis. (2019) Consequences of climatic thresholds to fire activity and post-fire vegetation change. USFS Missoula Fire Lab Seminar Series, Missoula, MT.

Appendix C: Metadata

This project produced a dataset containing annually-resolved establishment dates for ponderosa pine and Douglas-fir seedlings and saplings, associated plot data (understory vegetation cover by life form, slope, aspect), and annual climate data at each plot for the years following the fire. The associated metadata file has been submitted to JFSP and the data and metadata are publicly available through Dryad at:

Davis, Kimberley T. et al. (2019), Data from: Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration, Dryad, Dataset, <https://doi.org/10.5061/dryad.pc3f9d8>