



A climatic dipole drives short- and long-term patterns of postfire forest recovery in the western United States

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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.

climate variability | wildfire | conifer recovery | drought | Rocky Mountains

Concern is mounting that climate change and altered disturbance regimes may hinder forest regeneration across western North America. Large stand-replacing fires and rapid succession reburns limit seed sources while postfire climatic conditions are increasingly becoming untenable for regeneration, especially for seed-obligate species (1, 2). More broadly, we know from multiple lines of evidence—the paleoecological record (3, 4), present-day observations (5, 6), in situ experiments (7), and future projections (8, 9)—that stand-replacing disturbances coupled with climatic changes may trigger dramatic transformations in forested systems (10).

Spatial climate gradients have been used as a proxy for anticipated climatic changes. For example, space-for-time substitutions are commonly used to infer how climate change may affect recruitment. But growing research efforts that directly address postfire climatic conditions (e.g., multiyear drought) suggest that temporal climatic variability can rival or override the importance of spatial climate gradients in predicting juvenile recruitment (11, but see refs. 12–14). Indeed, within and across climatic domains of the western United States, postfire drought has been implicated as a dominant constraint on postfire conifer recovery (6, 15). Even if average climatic conditions, which vary

spatially, do not—or do not yet—exceed limiting or lethal thresholds, periods of unfavorable conditions (e.g., multiyear drought) may compromise juvenile recruitment (16). Just as drought may leave a legacy on trees' biological functions and growth as well as on forest productivity and mortality (17, 18), it may also have long-term implications for forest recovery by constraining juvenile recruitment.

Climatic teleconnections and regional circulation regimes facilitate large-scale climatic anomalies on interannual to decadal timescales such that temporal variability in conditions may also have a spatial fingerprint. For example, shifts in the storm track with the El Niño–Southern Oscillation (ENSO) lead to a latitudinal precipitation dipole in the cool season between the Pacific Northwest and the Southwest of the United States (19, 20). Although the influence of the temporal variability associated with particular phases of climatic modes (e.g., ENSO) has been demonstrated in forest and fire ecology (e.g., refs. 21–23), the implications of climatic dipoles per se on ecological dynamics is a nascent area of inquiry (24). For example, Strong et al. (25) correlated two modes of North American boreal bird irruptions with climatic dipoles. Dong et al. (26) linked forest drought sensitivity to a climatic dipole within California. In Europe, a growing east–west contrast in tree growth sensitivity has been attributed to the intensification of a precipitation dipole across

Significance

Rising temperatures and increasing drought may compromise ecosystems' abilities to recover from disturbance. This study reveals how recurring, large-scale patterns in drought variability have short- and long-term effects on forest recovery from wildfire in the western United States. Annual juvenile ponderosa pine recruitment in the Northern Rockies and Southwest tracks a north–south climatic dipole that emerges approximately every 4 y and renders one region anomalously dry and the other anomalously wet. Anomalously dry conditions inhibit postfire recruitment in the short-term and shape recovery trajectories decades later. To date, the influence of climatic dipoles on large-scale, enduring patterns of forest recovery has remained largely unexplored and may improve predictions of both ecosystem transformations and species range dynamics under climate change.

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the Mediterranean basin (27, 28). Nevertheless, we know of no studies that examine how climatic dipoles may influence forest recovery trajectories. In particular, we may expect the influence of a climatic dipole on such trajectories to be amplified if climatic conditions increasingly exceed limiting thresholds for regeneration—a trend already underway in some contexts (Fig. 1 and 15, 16, 29).

The temporal dynamics of climatic dipoles unfold on inter-annual to decadal timescales (24), which compels us to broaden the temporal lens at which we examine postfire recovery. Although there are growing efforts to examine juvenile recruitment at extended intervals since fire, much postfire sampling occurs soon after fire. For example, 36% of sampling efforts reported in the literature occurred within the first 5 y postfire, and 55% occurred within the first decade (SI Appendix, Fig. S1). Short interval sampling may obscure longer-term trends in recruitment probabilities (e.g., stabilization) and limit the time period over which one may draw inferences about the enduring influences of postfire climatic variability. Furthermore, there are limited data on annually resolved establishment rates (but see refs. 14, 15, 30–32). Most postfire sampling quantifies juvenile density or presence instead of annual establishment rates. And yet, recovery trajectories are the integration of discrete recruitment events, the rates of which vary in time. Indeed, there is a need to link annual recruitment probabilities with cumulative recruitment probabilities over extended intervals to resolve the influence of climatic variability on mechanisms that underlie recovery trajectories.

Here, we show that a climatic dipole spanning the Interior West shapes large-scale postfire conifer recovery both annually and over the longer term. We focus on postfire juvenile recruitment dynamics of two widespread and economically important conifer species: ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga*

menziesii). Specifically, we 1) identified the recurring spatial structure of climatic moisture deficit (CMD) anomalies as a north–south dipole. 2) We then examined how the strength of this dipole postfire shapes annual juvenile recruitment. We did so by leveraging annual recruitment probability models derived from annually resolved establishment dates determined via destructive sampling and aging in the northern Rocky Mountains (NR) and southwestern US (SW) (15). 3) Lastly, we examined the influence of postfire conditions on long-term cumulative juvenile recruitment probabilities (i.e., probabilities of juvenile presence) using data from 989 Forest Inventory and Analysis (FIA) program (33) plots within 431 fires that burned over the past three decades. We show that annual recruitment probabilities of ponderosa pine in the NR and the SW track the CMD dipole and that postfire drought conditions have implications for cumulative recruitment probabilities multiple decades after fire. Our findings imply that the immediate and lasting legacy of spatiotemporal climatic variability on forest recovery requires broadening the spatial and temporal lens through which we examine postfire juvenile recruitment (34, 35).

Results and Discussion

A strong north–south dipole in growing-season CMD anomalies recurred across the Interior West from 1980 to 2019, with both immediate and lasting implications for regional postfire forest recovery trajectories (Fig. 2). Moreover, this pattern was overlaid on an ongoing, directional drying trend across the domain (36, 37). Annual postfire juvenile ponderosa pine recruitment probabilities in the NR and in the SW declined with this domainwide drying (first principal component [PC1], Sen’s slope $\sigma = 1.02$) while tracking the strength of the CMD dipole index (second principal component [PC2]).* Under conditions that were anomalously dry in the NR and moist in the SW (corresponding to a negative PC2), ponderosa pine was less likely to establish in the NR than in the SW relative to regional averages, and vice versa (corresponding to a positive PC2). More specifically, annual recruitment probabilities in the NR and in the SW were similarly correlated with the domainwide drying trend ($\rho = -0.598$ and $\rho = -0.368$, respectively) and correlated in opposing directions with the CMD dipole index ($\rho = 0.378$ and $\rho = -0.441$, respectively). Regional differences in correlation strength may be attributed to the higher aridity of the SW, where average conditions are closer to lethal climatic thresholds than in the NR (15), hence a more pronounced sensitivity to the CMD dipole.

Distinct regional recruitment pulses corresponded with strong manifestations of the dipole (defined as PC2 exceeding a magnitude of 1; Fig. 3). During our study period, one such strong dipole manifestation occurred at least once every 4 years (mean interval of 2.92 y, SD = 1.01). This strong dipole emergence is likely attributable to modulations in the North American monsoons with corresponding effects on the summer precipitation regime, particularly in the SW (38). Additionally, shifts in cool-season precipitation related to ENSO and Pacific interdecadal variability lead to spatial contrasts in snowpack (19, 20, 39), which may amplify growing-season CMD anomalies (40). These, in turn, shape recruitment dynamics. Our study period (1980 to 2019) does not afford sufficient time to definitively determine how these broader modes of climatic variability may underpin the CMD dipole and its effect on recruitment. Nevertheless, the CMD dipole is consistent with the previously identified latitudinal precipitation dipole between the Pacific Northwest and the Southwest (19, 20). Further, our results show that severe deficit conditions constrained annual ponderosa pine recruitment rates in the NR and

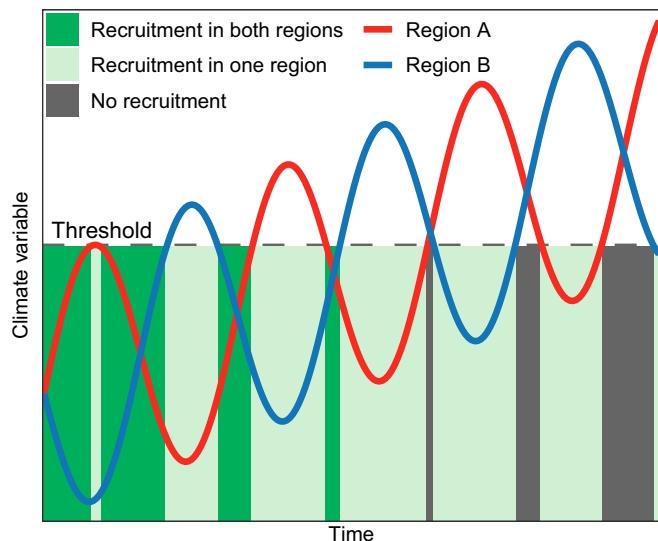


Fig. 1. Conceptual model showing recruitment consequences in two regions at opposing ends of a climatic dipole under warming. Under an active climatic dipole, two distant regions may experience opposing conditions in a climate variable that may limit conifer recruitment (e.g., climatic moisture deficit). So long as conditions in both regions remain below a lethal threshold in that climate variable (dashed gray line), recruitment may occur in both regions (as indicated in dark green). As directional changes in that climate variable occur over time (e.g., warming and drying), one or both regions may exceed that threshold at a given time. This will depend on the orientation and strength of the climatic dipole—for example, cool, moist conditions in the SW may be conducive to recruitment while concurrent hot, dry conditions in the NR inhibit recruitment, or vice versa. Eventually, conditions in both regions may be untenable for conifer recruitment (as indicated in gray regions).

*In contrast to annual postfire ponderosa pine recruitment probabilities, Douglas-fir recruitment did not track the CMD dipole across the Interior West. We hereafter focus this discussion on ponderosa pine dynamics and primarily describe Douglas-fir dynamics in SI Appendix.

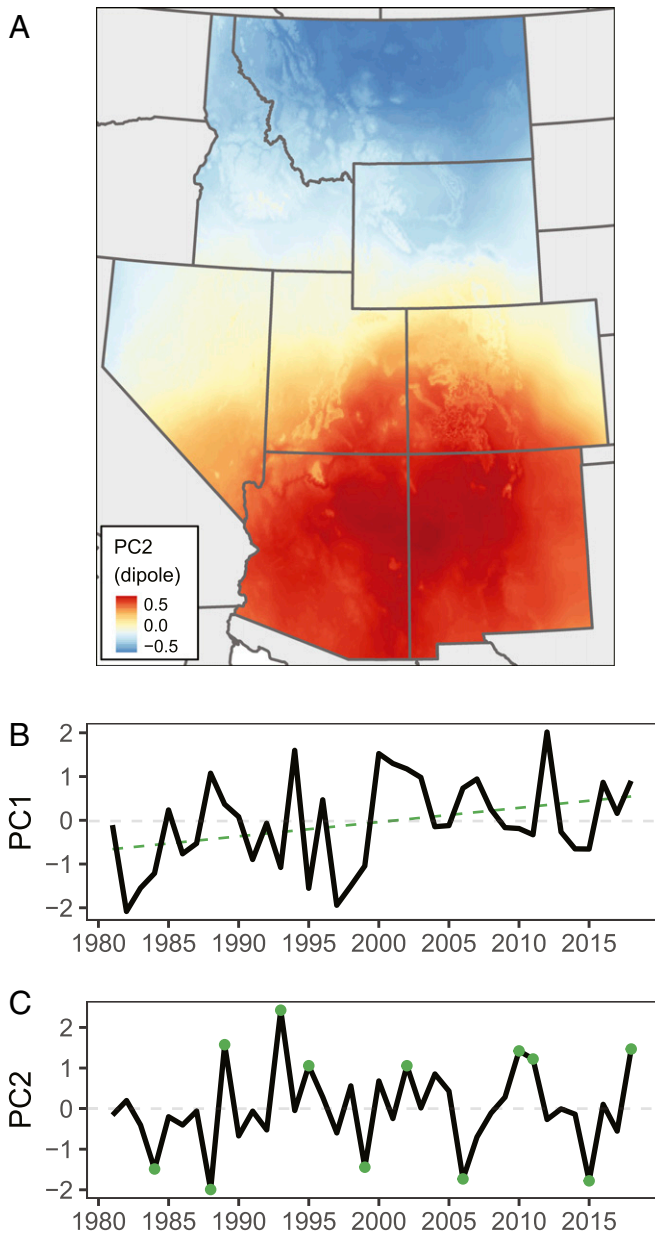


Fig. 2. Spatial and temporal decomposition of May to September climatic moisture deficit (CMD) anomalies. The first principal component (PC1; not mapped) expresses the dominant mode of variability in CMD anomalies as a regionwide average, capturing 42.7% of the variability in CMD anomalies. (A) The second principal component (PC2) reveals a strong north-south dipole across the study area that accounts for 21.1% of the variability. (B and C) The temporal decompositions of PC1 and PC2 are expressed as time series indices, with values on the y axis indicating the degree to which the pattern is manifest in any given year. PC1 shows an increasing trend over time (green dashed line), indicative of directional drying across the domain (Sen's slope $\sigma = 1.02$). PC2 was particularly strong (defined as exceeding a magnitude of 1; green points) for 12 y of our study period: in 5 y there were anomalously low deficits in the Southwest (moist) and high deficits in the Northern Rockies (dry; $PC2 < -1$) while in 7 y there were anomalously low deficits in the Northern Rockies (moist) and high deficits in the Southwest (dry; $PC2 > 1$).

the SW, and these regional rates diverged when the CMD dipole across the Interior West was strong.

Severe dry conditions constrain ponderosa pine regeneration such that the tempo of the CMD dipole may indicate the frequency at which critical recruitment thresholds may be exceeded.

Indeed, large-scale, recurring modes of drought variability may have relevance in other arid forest systems under climate change. The differential effects of geographic polarities in drought on annual forest growth have been demonstrated (26–28) and the effects of climatic dipoles on tree masting have been inferred (25). But the short-term and lasting influence of such a dipole on recovery dynamics has not yet been characterized. Importantly, because climatic dipoles span vast distances, the postfire trajectories of ponderosa pine stands thousands of kilometers apart may be intrinsically linked by this dipole, even if in opposing directions.

Climatic Variability and Annual Recruitment Rates. Theory suggests that if a climatic threshold that strongly constrains recruitment is intermittently crossed, recruitment rates will accordingly rise and fall (16). Indeed, observations show conifer recruitment pulses occur under favorable conditions at multiple temporal scales in diverse forest systems. For example, dendrochronological reconstructions link pulses of tree establishment in arid forests to annual and decadal-scale periods that are cooler and moister (23, 41, 42). Postfire drought is increasingly implicated in constraining regeneration, whereas periods and locations that experience cooler, moister postfire conditions have more robust regeneration (6, 30, 31). More pointedly, field observations have quantified a nonlinear response to annually resolved vapor pressure deficit (VPD) and soil moisture for ponderosa pine regeneration: annual recruitment rates covary with fluctuations above and below critical VPD and soil moisture thresholds (15). In linking these climate-sensitive, annual recruitment probabilities to both directional drying and the periodic emergence of a

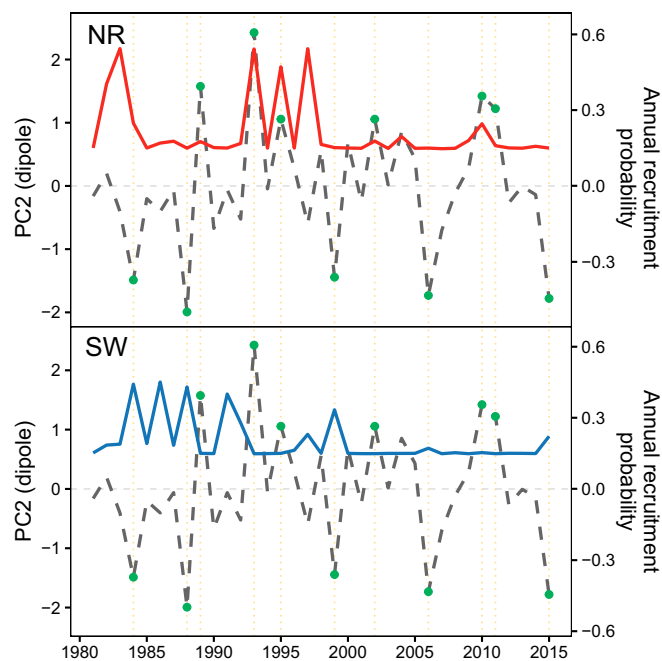


Fig. 3. Annual recruitment probabilities in the Northern Rockies (NR; red line) and Southwest (SW; blue line) tracked the strength of the CMD dipole (PC2; gray dashed lines) in opposing directions. Bootstrapped Spearman correlation coefficients between PC2 and annual recruitment probabilities were $\rho = 0.378$ for the NR and $\rho = -0.441$ for the SW. Several recruitment pulses in each region corresponded with strong manifestations of the dipole (defined as PC2 exceeding a magnitude of 1; green points and dotted orange lines) during which favorable (cooler, moister) conditions occurred therein. The domainwide PC2 time series is shown to convey the trend across Interior West, and correlations reflect site-specific PC2 values averaged for the NR and the SW.

CMD dipole, we clarify the tempo of these fluctuations that are critical for short- and long-term recruitment success.

Given interannual variability, one would expect climate-linked recruitment pulses to unfold even in the absence of a warming trend. Overlaid upon directional warming and drying (36, 37), critical thresholds related to lethal hydraulic stress will be increasingly surpassed (29, 43, 44). Indeed, transitions in annual recruitment probabilities have been quantitatively identified across the western US: average conditions in the SW crossed a critical moisture balance threshold in 1991 and the NR did so in 1996 (15). This corresponds with the directional drying trend observed herein (PC1; Fig. 2B) and the correlated decline in regional recruitment probabilities (Fig. 3). That said, under an active dipole, anomalously dry conditions in one region typically correspond with more moisture in the opposing region, potentially affording a relatively favorable window of opportunity for recruitment. Nevertheless, directional warming means that moisture demands for successful recruitment in many settings will be increasingly unmet. Even if average conditions remain tenable for years to come, the regular emergence of strong deficit anomalies will continue to ratchet systems away from conditions suitable for postfire regeneration (Fig. 1) (16, 45). As a result, the on-going erosion of areas that can support ponderosa pine recruitment is likely to occur.

Enduring Impact of a CMD Anomaly Dipole. The influence of CMD anomalies on annual recruitment probabilities imparted a lasting effect on cumulative recruitment probabilities (i.e., likelihoods of juvenile ponderosa pine presence) multiple decades postfire. When the maximum deficit anomaly[†] exceeded 1 SD and neared 1.75 SDs (roughly corresponding to the 50th and 90th percentile values of maximum deficit anomaly), ponderosa pine juveniles were 1/4 and 1/3 less likely to be present several decades postfire compared to moister postfire conditions with low deficits (Fig. 4). Thus a single very dry year soon after fire substantially reduced longer-term likelihoods of juvenile presence relative to postfire conditions that were more mesic. As with annual recruitment probabilities, this legacy effect of postfire drought was manifest spatially, following the CMD dipole. For example, between 2015 and 2017 the dipole was active such that areas of the SW (e.g., northern Arizona) experienced low deficits while the NR was exceptionally dry, particularly in 2015 and 2017. Following these conditions, we predict juvenile ponderosa pine are less likely to be present in the NR a decade postfire than in much of the SW (Fig. 5) despite higher average temperatures and less average precipitation in the SW relative to the NR.

The postfire period therefore represents a critical window in which vital processes must unfold, including ponderosa pine seed germination (for which warm, moist soil is required) and rapid taproot establishment in the face of competing grasses, shrubs, and other sprouting species (46, 47). Thus, an active climatic dipole may help set the stage for other contingencies (e.g., competitive exclusion) that constrain ponderosa pine recruitment, leaving a lasting fingerprint on the likelihood of juvenile ponderosa pine presence. It is important to note in our results, however, that the probability of juvenile presence postfire increased for several decades after an initial lag and then stabilized, reinforcing the notion that recovery is a protracted process (48, 49). Nevertheless, even if long-term stand conditions (e.g., juvenile densities) cannot be precisely inferred from initial stand conditions (50, 51), our findings suggest that postfire deficit

[†]Maximum deficit anomaly is defined as the maximum May–September CMD z-score that occurred at a plot within the first 3 y after fire; the 3-y span was determined quantitatively during model calibration and is consistent with the interval used elsewhere (e.g., refs. 6 and 31).

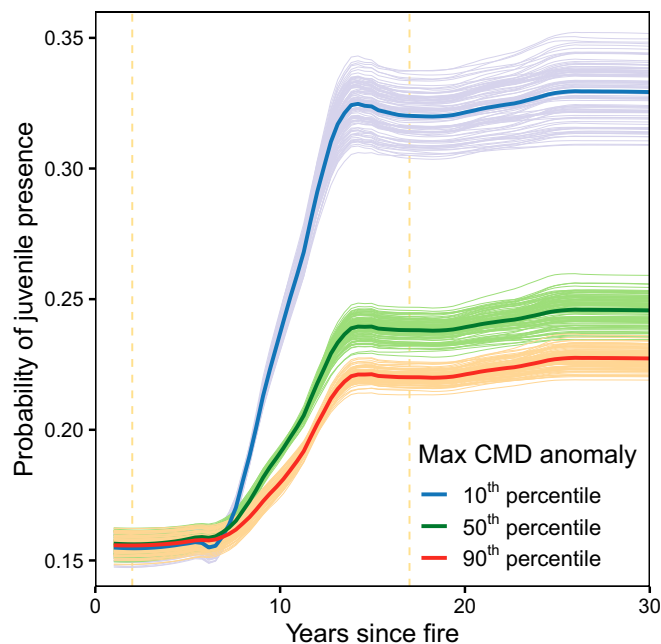


Fig. 4. The marginal influence of time since fire and maximum deficit anomaly, with the latter held at the 10th, 50th, and 90th percentile values, on the cumulative recruitment probability of ponderosa pine (i.e., probability of juvenile presence). Pale lines of each color represent the empirical distribution of outputs from 100 boosted regression tree model runs (smoothed with a span of 0.25) and the darker line is the mean of those outputs (smoothed with a span of 0.25). Dashed orange lines bound the 10th and 90th percentiles of years since fire. Average AUC across 100 model runs was 0.77.

anomalies—which regularly manifest in a cross-region dipole—will shape long-term cumulative recruitment probabilities.

Other nonclimatic factors also shape cumulative recruitment probabilities—the passage of time, as noted above, being chief among these factors (SI Appendix, Fig. S2). Juvenile presence for both ponderosa pine and Douglas-fir was strongly contingent on live, conspecific basal area, which corresponds with lower fire severities and greater seed availability. This positive influence persisted over time: immediately postfire as well as two decades after fire, predictions for plots with high basal area were strongly differentiated from those with lower basal areas (SI Appendix, Figs. S3–S6). For Douglas-fir, more live basal area likely afforded microclimate buffering that exceeded the importance of postfire drought—and therefore the CMD dipole—in driving juvenile Douglas-fir presence (52, 53). Broadly, this illustrates that species autecology, phenotypic variability, and individualistic responses to climatic variability (54, 55) challenge our ability to generalize across species with regards to recovery dynamics.

Context Dependencies at Multiple Scales. Postfire ponderosa pine and Douglas-fir recruitment patterns across the Interior West reflect a complex convergence of ecological and climatic dynamics that operate on multiple spatiotemporal scales. At the finest spatiotemporal scale, recruitment of either species is governed by contingencies related to the disturbance itself. For example, fire severity and burn patterns largely dictate the abundance and proximity of surviving trees that serve as seed sources (52, 56). For ponderosa pine, unfavorable anomalies in CMD reduce juvenile recruitment. At face value, the importance of these site-specific ecological and climate dynamics suggest that postfire recovery is strongly context dependent. However, even localized contingencies may be linked across vast areas via climatic teleconnections or regional circulation regimes. This means that postfire trajectories are not only dependent on local

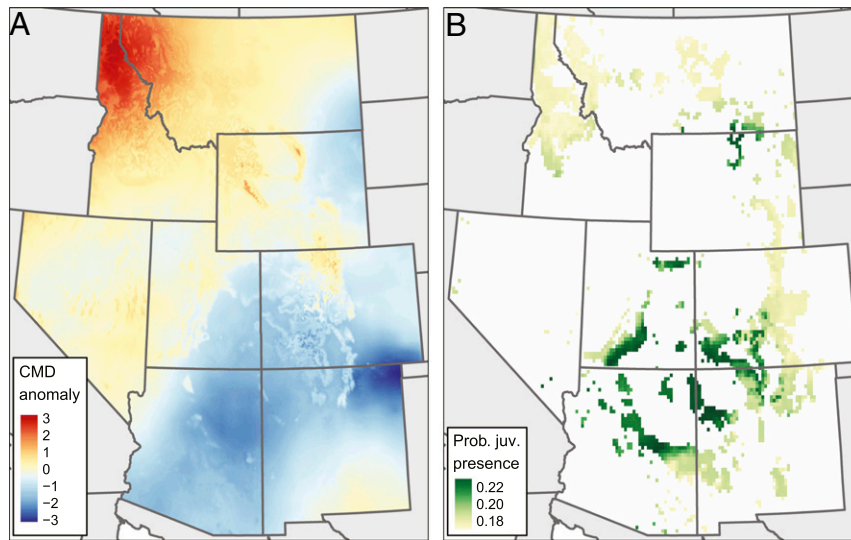


Fig. 5. (A) May to September CMD anomalies that occurred in 2015 illustrate a strong dipole ($PC2 < -1$) in which the Northern Rockies was particularly dry while parts of the Southwest experienced cooler and moister conditions than usual. (B) Predictions of juvenile ponderosa pine presence across the species' range 10-y postfire with CMD anomaly maxima based on 2015 to 2017 conditions (2016 and 2017 conditions given in *SI Appendix, Fig. S12*). In using the model to generate these spatial predictions (*SI Appendix, Fig. S11B*), maximum temperature varied in space while time since fire was held constant at 10 y, live conspecific basal area was held constant at the mean across the study area ($6.57 \text{ m}^2 \text{ ha}^{-1}$), and fire severity was held at the study area's mode of 2 (low severity). Predictions are averaged from 100 model runs.

context, but they are also embedded within synoptic climate dynamics that operate at much larger scales. This broader context is temporally coherent, even if characterized by internal contrasts (24, 57). When broader contexts are obscured, we risk detecting artifacts of scale instead of actual ecological patterns (58). For example, a localized or regional study that unfolds during a cool, moist period and documents robust recovery could draw conclusions about climate change impacts that misrepresent contemporaneous recruitment failures elsewhere, as may occur under a strong CMD dipole.

Explicitly addressing these broader spatial and temporal contexts in which disturbance and recovery unfold may improve our ability to predict and plan for both. For example, fire activity in the western US has been linked to modes of climatic variability (e.g., ENSO) both prior to and concurrent with a given fire season (59, 60). Similarly, broad-scale dipoles in moisture limitations that lag or coincide with conditions that amplify fire activity in dry conifer systems may indicate where postfire juvenile recruitment will be most constrained. These influences are not entirely distinct: the climatic conditions that amplify fire activity likely correspond with stressful conditions that constrain regeneration, especially of seed-obligate species. But the sequential relationship and contingencies associated with both processes—disturbance and recovery—call for parsing the role of climatic variability on each to improve predictions or forecasts. It is important to note, however, that uncertainties in how modes of climatic variability evolve under climate change may limit the scope of such forecasts (22, 61).

On a biogeographic scale, interannual and decadal modes of climatic variability may clarify our understanding of range dynamics, including apparent lags in anticipated range shifts (62, 63). These apparent disequilibria are based on average climatic conditions (e.g., 30-y normals), which may obscure critical fluctuations that occur on finer timescales and that are more closely aligned with the vital rates of juveniles. Accordingly, species responses to prevailing climate trends must be discerned from higher frequency variability in climatic conditions as well as spatial linkages in that variability (e.g., climatic dipoles). For example, the CMD dipole examined here is particularly strong every 3 to 4 y on average, often alternating in its polarity. This

implies that both the leading (northern) and the trailing (southern) edges of ponderosa pine's range regularly experience conditions that strongly limit recruitment. This may expedite range contractions at both edges, particularly at lower elevations and in moisture-limited settings (29, 64). On the other hand, the periodic moist conditions that arise under an active dipole may afford windows of opportunity for continued, if occasional, recruitment in marginal areas, as well as opportunities for colonization at range edges (16, 65). Nevertheless, directional warming and the ongoing exceedance of critical thresholds may shrink these windows of opportunity, even at leading edges (66, 67). Such implications of multiscale spatiotemporal climatic variability on species ranges must be further tested at biogeographic scales and requires considering other filters such as dispersal constraints, landscape connectivity, available habitat, and edaphic factors that affect species persistence (recovery) and range shifts (68–70).

Here, we show that annual recruitment probabilities track a large-scale climatic dipole and that this sensitivity is manifest in long-term patterns of juvenile presence. Importantly, multiyear anomalies may set sites on enduring and opposing trajectories that contrast with expectations based on spatial climate gradients alone. For example, stressful anomalies in an otherwise cool and moist climate may undercut near- and long-term recruitment probabilities while a typically hotter, drier region may be set on a robust recover trajectory. Furthermore, these trajectories may continue to diverge for multiple decades after fire before stabilizing, which cautions against prematurely concluding the fate of a postfire system. Rather, monitoring postfire stand conditions—including juvenile mortality as well as recruitment into the overstory, which we do not capture here—and characterizing climatic variability at multiple scales will help us attribute ecological dynamics to climatic changes. Such clarity will help us understand where and when interventions to support recovery may be fruitful and where and when we may need to accept fire-catalyzed transformations.

Methods

Climate Data and Dipole Analysis. We used monthly average maximum temperature, total precipitation, and CMD at $1/24^\circ$ resolution ($\sim 4 \text{ km}$) from TerraClimate (71). CMD is evaporative demand not met by available water

(rain plus snowmelt) and accounts for water-holding capacity in mid-upper soil layers. Deficit is therefore a biophysically meaningful surrogate for drought (72). We used 30-y normals (1981 to 2010) to capture spatial variability in climate across the Interior West.

To examine temporal variability in drought conditions, we computed annual May through September CMD z-scores from 1980 to 2019. These values reflect how anomalous the growing season deficit was at a given location for any given year. We identified the spatial and temporal structure of a CMD climatic dipole across the Interior West using principal component analysis (PCA) (73). For a two-dimensional dataset—here, including time and space—PCA defines a set of spatial structures that concisely captures the variance within that dataset; these are expressed as principal components (PCs) with a corresponding time series index. The first principal component (PC1) captured 42.7% of the variability in CMD anomalies as a regionwide average, which is to be expected for a domain of this spatial extent (i.e., relatively small in the context of atmospheric circulation (74, 75)). The second principal component (PC2) captured 21.2% of the variability and revealed a strong north–south dipole. Although PCA is widely acknowledged to be sensitive to the geographic domain, we found the dipole pattern also emerged when we considered an expanded domain of western North America. We further substantiated the dipole through one-point correlation analysis of CMD anomalies across the domain that excluded the influence of PC1 (*SI Appendix, Fig. S7*). Temporally, the dipole was particularly strong (defined here as the absolute value of $PC2 > 1$) for 12 y of our study period: 5 y had low deficits in the Southwest (moist) and high deficits in the Northern Rockies (dry) while 7 y had the opposite (*Fig. 2*). We compared the PC1 and PC2 time series to annual recruitment probabilities to examine how spatial patterns of recruitment corresponded to the regionwide drying trend as well as the strength and frequency of the dipole (described below).

In our models to predict likelihood of postfire juvenile presence (described below), we used the maximum May–September CMD z-score (hereafter “maximum deficit anomaly”) that occurred within the first 3 y after fire at a plot. If plots were inventoried fewer than 3 y postfire, we used the maximum z-score that occurred within that fire-to-inventory interval. We explored average and maximum z-scores at multiple intervals postfire and found the 3-y maximum to perform best in our models (described below; model skill was similar when 1-, 2-, and 4-y maximum z-scores were used). Furthermore, the use of deficit within a 3-y timespan is consistent with prior studies (e.g., refs. 6 and 31). Because we used maximum z-scores, these values were not centered on zero. Although a directional warming trend would suggest an increase over time in z-scores computed from the same baseline, there was no increase in maximum deficit anomalies over the study period (*SI Appendix, Fig. S8*).

Annual Recruitment Model. We examined postfire juvenile conifer recruitment in two ways: leveraging annual recruitment probability models based on annually resolved establishment data (15) and using juvenile presence data (i.e., cumulative recruitment probabilities) from the US Forest Service’s FIA program (33). Davis et al. (15) destructively sampled 2,820 juvenile ponderosa pine and Douglas-fir that had established after 33 wildfires in the western US (at 40 sites in the NR and 21 sites in the SW, among other regions) to determine precise germination years. Such aging data are, of course, only available for extant juvenile trees, and so do not capture mortality. However, these data do reflect temporal variability in successful conifer establishment and therefore indicate annual recruitment probabilities. Davis et al. (15) constructed boosted regression tree (BRT) models to predict these annual recruitment probabilities (for 1981 to 2015) as a function of annual climatic conditions during the year of germination and other biophysical variables. For both species, the final predictor set for these models included distance to seed source, fire severity, and time since fire, as well as soil moisture of the driest month and vapor pressure deficit for ponderosa pine and spring soil moisture and maximum land surface temperature for Douglas-fir. Full details regarding parameterization and evaluation of these recruitment probability models are given in Davis et al. (15). To examine whether recruitment tracked the strength and prevalence of the regional drying trend (PC1) and the CMD dipole (PC2), we compared annual recruitment probabilities for each species to time series of PC1 and PC2, averaged from site-specific PC values (40 sites in the NR and 21 sites in the SW). We specifically examined these relationships for the NR and the SW, as the dipole is characterized by opposing conditions in these two regions. To maintain clarity regarding this opposing pattern, and for consistency with the signage of the domainwide PC2, we used the inverse of the averaged site-specific PC2 values in the NR. We applied a bootstrap approach (1,000 replicates) to Spearman correlation analyses to examine whether recruitment pulses were exerting substantial

leverage on the results. To further illustrate these relationships, we plotted NR and SW recruitment probabilities against PC1 and PC2 and applied a simple linear regression (*SI Appendix, Fig. S9*). Using the Ljung and Box (76) and Kwiatkowski–Phillips–Schmidt–Shin (77) tests, we confirmed there was no significant temporal autocorrelation in these annual recruitment probabilities or in PC2 that would compromise Spearman correlation.

Juvenile Presence (Cumulative Recruitment) Model. To extend the spatial and temporal scope of our inquiry, we used the FIA database to examine postfire juvenile presence (i.e., cumulative recruitment probability) at multiple intervals since fire. Details regarding FIA data collection, processing, management, and evaluation are given in Bechtold and Patterson (33). We used FIA plots that burned in fires recorded by the Monitoring Trends in Burn Severity program (MTBS) (78) and were inventoried postfire—that is, only plots that burned since 1984 and were subsequently inventoried at any point. If a plot burned multiple times within the MTBS record, we noted that the plot experienced a reburn, but retained only data associated with the most recent fire. Similarly, if a plot was inventoried multiple times, we retained only the most recent inventory data. We excluded plots with evidence of human disturbance or planting.

We retained burned plots with live or dead standing ponderosa pine or with downed ponderosa pine that had been standing during prior inventories (hereafter, “ponderosa pine plots”) and similarly retained plots for Douglas-fir (hereafter, “Douglas-fir plots”). Per these criteria, we analyzed 521 plots for ponderosa pine with fire years and inventory years ranging from 1984 to 2012 and 2002 to 2015, respectively. For Douglas-fir, we analyzed 692 plots with fire years and inventory years ranging from 1984 to 2012 and 2002 to 2016, respectively. There were 224 plots where the species co-occurred and which met our criteria; these plots were used in analyses for both species. In sum, we examined 989 unique plots on 431 unique fires across the Interior West (*SI Appendix, Fig. S10*). For each plot, we converted juvenile ponderosa pine and Douglas-fir tallies—which include individuals less than 2.5 cm in diameter—to presence/absence to reconcile the considerable variability in juvenile densities across the study domain (*SI Appendix*).

We sought to examine the influence of time since fire, climatic variability, and plot-specific characteristics on the likelihood of juvenile presence. More specifically, predictors included the climatic variables described above, the interval between the year of fire and the year of inventory, whether the fire was a recent reburn (since 1984, given the extent of the MTBS record), fire-severity class (i.e., unburned, low, moderate, high severity) as reported by MTBS, duff and litter depths, and live conspecific basal area (*SI Appendix, Table S1*). We did not consider topographic variables (e.g., elevation), because such topographic effects on growing conditions would be confounded with latitude, and they did not emerge as strong predictors during preliminary exploration. It is important to note that we modeled the influence of these variables on the likelihood of juvenile presence in the postfire inventory year and not the likelihood of recruitment in any given year. In other words, our binary response variable—juvenile presence—reflects the cumulative probability that a juvenile established and was on site at the time of the FIA inventory. (By contrast, the annual recruitment probabilities [described above] do reflect the likelihood of recruitment in any given year.)

We used BRTs to model relationships between our predictor variables and juvenile presence of each species (*SI Appendix, Fig. S11A*). We evaluated multiple parameterizations of the BRTs to optimize model skill (following ref. 79), conducting all modeling with the R package *dismo* (80). Our final models used a learning rate of 0.001, which shrinks the contribution of each additional tree to the growing model, and a bag fraction of 0.75, which controls model stochasticity by drawing 75% of the full training dataset at random, without replacement, at each tree-building step. We constrained tree complexity to a maximum interaction order of three to minimize overfitting. We used the *gbm.step* function, which implements an internal cross-validation procedure using the specified bag fraction to identify the optimum number of trees, given the learning rate and tree complexity (79). Because of model stochasticity, we built 100 models for each species to evaluate variability across runs and to inform our confidence in emergent patterns. To reduce overfitting and build the most parsimonious models, we systematically evaluated how the removal of each variable affected model performance per the area under curve statistic (AUC) from the receiver operating characteristic curve (ROC) (following ref. 81). In our final models for each species, we retained the variable set that maximized AUC (*SI Appendix*). To evaluate how each variable in the final set influenced the likelihood of juvenile presence, we iteratively implemented the models while holding all but one variable constant, then plotted the predicted responses in partial dependence plots.

To demonstrate how the CMD dipole may have a legacy effect on longer-term likelihoods of juvenile presence, we projected these likelihoods after a time period (2015 to 2017) that exhibited a strong polarity in deficit anomalies across the Interior West (SI Appendix, Figs. S11B and S12). Assuming an enduring legacy effect of postfire drought on longer-term likelihoods, the signature of the climatic dipole should be manifest in contrasting likelihoods of juvenile presence across the Interior West. (We projected only ponderosa pine juvenile presence because our final model for this species included the deficit anomaly variable, whereas our Douglas-fir model did not.)

Data Availability. The forest inventory and climate data used in this study are publicly available via the USDA Forest Service's Forest Inventory and Analysis

Program at <https://www.fia.fs.fed.us/> and the TerraClimate database at the University of Idaho Northwest Knowledge Network (<https://data.nkn.uidaho.edu/dataset/monthly-climate-and-climatic-water-balance-global-terrestrial-surfaces-1958-2015>; DOI: 10.7923/G43J3B0R). The code is publicly available at GitHub, <https://github.com/CaitLittle/fia-regen>.

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