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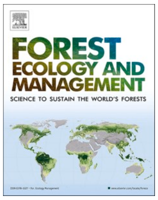

Western larch regeneration more sensitive to wildfire-related factors than seasonal climate variability

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ABSTRACT

To understand the impacts of changing climate and wildfire activity on conifer forests, we studied how wildfire and post-fire seasonal climate conditions influence western larch (*Larix occidentalis*) regeneration across its range in the northwestern US. We destructively sampled 1651 seedlings from 57 sites across 32 fires that burned at moderate or high severity between 2000 and 2015; sites were within 100 m of reproductively mature western larch. Using dendrochronological methods, we estimated germination years of seedlings to calculate annual recruitment rates. We used boosted regression trees to model the annual probability of recruitment as a function of (i) 'wildfire-related factors' including distance to seed source, satellite-derived fire severity, and time since fire, and (ii) seasonal climate conditions, including variables reflecting temperature and water availability. Most recruitment occurred within five years after wildfires, at sites within 25 m of reproductively mature western larch trees. Wildfire-related factors had the highest relative influence (87 %), while post-fire seasonal climate had less influence (13 %) on post-fire recruitment. Annual recruitment probability increased with growing season actual evapotranspiration, to a maximum of c. 275 mm, and then decreased. Annual recruitment probability decreased as growing season climatic water deficit increased. Our results suggest that recent climate trends – increased growing season water deficit and decreased actual evapotranspiration – have had variable, yet net-neutral, impacts on the climate suitability for post-fire western larch regeneration across its range. Climate suitability increased modestly at 'cooler-and-wetter' sites and decreased modestly at 'warmer-and-drier' sites. The strong influence of wildfire-related factors highlights the potential for management decisions to promote western larch in recently burned areas. Facilitating prescribed or managed wildfire with moderate- to high-severity patches will generate conditions suitable for natural regeneration, provided sufficient seed sources survive the fire. Additionally, our findings support monitoring of natural regeneration or augmenting regeneration by planting within the first five years after fire, consistent with current management practices.

1. Introduction

Warmer and drier climate is impacting forest ecosystems directly, through controls on tree regeneration (Davis et al. 2019, Young et al. 2019) and mortality (Lloret & Kitzberger, 2018; Van Mantgem et al., 2009), and indirectly, through more frequent and severe wildfires (Abatzoglou & Williams, 2016; Littell et al., 2018; Parks & Abatzoglou, 2020). Across Western North America, many tree species have coexisted with fire for millennia, exhibiting trait-mediated resistance and resilience to wildfires (Hessburg et al., 2019; Johnstone et al., 2016; Stevens et al., 2020). For example, thick bark increases the likelihood of a tree resisting mortality from low- and moderate-intensity surface fires, and serotinous cones facilitate resilience to wildfires through abundant post-fire tree regeneration (Cansler et al., 2020; Hood et al., 2021; Stevens et al., 2020). As climate and wildfire deviate from historical patterns, continued increases in area burned by stand-replacing (i.e., high-severity) fire are expected to catalyze climate-driven changes to forest ecosystems (Abatzoglou & Williams, 2016; Crausbay et al., 2017;

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Marlon et al., 2009; Parks et al., 2023; Parks & Abatzoglou, 2020).

Forest ecosystem response to a wildfire reflects interacting abiotic and biotic factors associated with the characteristics of the fire, the post-fire environment, and the life history traits of the species present (Chambers et al., 2016; Davis et al., 2018; Johnstone et al., 2016; Stevens-Rumann et al., 2018; Tepley et al., 2017). These factors determine if forests exhibit resilience to wildfire, the ability to recover to their pre-fire state (Holling, 1973), or if they alternatively undergo some level of post-fire reorganization (Seidl & Turner, 2022). In mixed-conifer forests of the western United States, wildfire plays an important role in stimulating tree regeneration by opening the canopy and generating suitable seedbeds for colonization (Crotteau et al., 2013; Johnstone & Chapin, 2006; Larsen, 1925). Yet increases in fire severity can limit post-fire seed availability, decreasing rates of post-fire tree recruitment (e.g., Donato et al., 2016; Kemp et al., 2016; Povak et al., 2020).

Once seeds are present, post-fire conifer regeneration is limited by seasonal-to-annual climate conditions (Coop et al., 2020; Davis et al., 2019, 2023; Haig, 1936; Harvey et al., 2016; Kemp et al., 2019; Stevens-Rumann et al., 2018). Seedlings are especially sensitive to stressful climates, making it a critical demographic stage determining post-fire forest regeneration success (Bell et al., 2014; Davis et al., 2018; Dobrowski et al., 2015). Following high-severity fire, wetter-than-average years are typically associated with increased seedling recruitment and survival, whereas warmer and drier years are associated with decreased recruitment and survival (Balducci et al., 2015; Crockett & Hurteau, 2022; Davis et al., 2023; Marsh et al., 2022; Rother & Veblen, 2016; Wolf et al., 2021). Warmer and drier conditions increase the likelihood of acute thermal cambial damage and cause higher seedling water demands, leading to a higher risk of hydraulic failure and carbon starvation (Helgerson, 1989; Isaac, 1943; Rank et al., 2022; Sapes et al., 2019; Smith & Silen, 1963). Climatic thresholds governing post-fire regeneration have been identified for ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), specifically among the warmest and driest portion of their geographic range (Davis et al., 2019; Hankin et al., 2019). It is less clear, however, if and how climatic thresholds govern regeneration of montane and subalpine species (although see Hansen & Turner, 2019), which can also be strongly limited by non-climatic factors, including competition and other biotic interactions (Ettinger & HilleRisLambers, 2013; Steed & Goeking, 2020).

Climate change is increasing the occurrence of warmer and drier years, and thus years when potential climatic thresholds to regeneration would be surpassed (Andrus et al. 2018, Davis et al. 2019). Quantifying the relationship between recruitment rates and seasonal climatic conditions helps reveal if and how the climate suitability for post-fire regeneration is changing. Individual species have distinct climate-recruitment relationships, implying that each will have a unique response to climate change (Davis et al., 2019, 2023; Lloret & Kitzberger, 2018; Stevens-Rumann et al., 2022). Thus, investigations of climate-recruitment relationships for individual species are essential to anticipate the response of forests to changes in climate and fire activity.

Western larch (*Larix occidentalis*) is a species of high ecological, cultural, and economic value in the inland northwestern United States ("Northwest") and Canada (Crotteau et al., 2019; Schmidt et al., 1976). Western larch is most abundant in areas of moderate moisture availability in mid-elevation forests, although it also co-occurs in dry forests in association with ponderosa pine and Douglas-fir. Western larch is often confined to northerly aspects within its distribution in the United States, which are characterized by cooler and wetter conditions than southerly aspects (Fiedler & Lloyd, 1995; Schmidt et al., 1976). In British Columbia (Canada), it can be more common on southerly aspects (Marcoux et al., 2015). Western larch is both highly fire-resistant, due to its thick bark, and fire-resilient in that it regenerates prolifically after fire with canopy opening and bare mineral soil exposure (Belote et al., 2015, Hopkins et al., 2014; Schmidt et al., 1976). It has been hypothesized that the past century of fire suppression and cessation of Indigenous burning has impacted the range of western larch by reducing opportunities for establishment (Fiedler & Lloyd, 1995; Steed & Goeking, 2020). Consequently, so long as seeds remain available after wildfires, western larch may be an increasingly common component of Northwest forests as burned area increases (Hessburg, 2016; Hoecker & Turner, 2022; Steed & Goeking, 2020). Alternatively, high-severity fire, which can kill mature western larch over large areas, may limit post-fire seed availability and thus inhibit post-fire regeneration (Crotteau et al., 2019).

We addressed three research questions concerning the influence of climate and wildfire on the annual probability of post-fire western larch recruitment across its range in the Northwest: (1) what is the relationship between seasonal climate conditions and the probability of western larch recruitment after wildfires; (2) how do seasonal climate variables compare in importance to other factors known to influence post-fire recruitment, such as seed availability, fire severity, and time since fire; and (3) how has the climate suitability for post-fire western larch regeneration changed over recent decades in the Northwest? We expected that the direct and indirect impacts of climate change could have contrasting effects on western larch recruitment. We hypothesized that increasing temperatures and decreasing moisture availability would limit post-fire western larch recruitment, while higher fire severity could promote western larch recruitment through increased access to mineral seedbeds and lower canopy cover. Our results highlight how shifting climatic and wildfire dynamics are influencing western larch regeneration across its range in the United States.

2. Materials and methods

2.1. Study region

Our study area spans the geographic distribution of western larch in the United States (Fig. 1). Western larch is found in mixed-conifer forests and extends into lower-elevation subalpine forests (elevation range of 400–2200 m); it is associated with *Pinus ponderosa* and *Pseudotsuga menziesii* in warmer and drier areas and *Pinus contorta*, *Abies grandis*, *Abies lasiocarpa*, *Picea engelmannii*, *Thuja plicata*, and *Tsuga heterophylla* in cooler and wetter areas. It occurs in mountainous terrain often characterized by steep topography. The region experiences warm, dry summers and cool, wet winters. Mean annual temperature, averaged across the study region, was 8.5 °C, and mean total annual precipitation was 657 mm (1981–2010 averages at 4-km pixel resolution; Abatzoglou et al., 2018). A total of 946 wildfires larger than 405 ha burned in the study region between 1986 and 2020, with a significant increase in the annual area burned and proportion of area burned at moderate severity over that period (Theil-Sen slope estimate, 1150 ha·yr^{-1} and 0.002·yr^{-1}, respectively; $p < 0.001$; Fig. 1). Proportion of "core area", defined as the proportion of total area burned that was >100 m from a low severity, moderate severity, or unburned patch (and presumably a seed source), did not change over time (Theil-Sen's slope = -0.0002 yr^{-1}, $p = 0.73$; Fig. 1).

2.2. Site selection

We selected sites that burned in wildfires between 2000 and 2015 and spanned the full climatic range of western larch in the US, using a stratified, random sampling design (Fig. 1). Sites were located in patches that burned at moderate or high severity, as classified using satellite-derived burn severity (i.e., > 180 dNBR; Parks et al., 2018) and verified in the field (i.e., > 25 % fire-caused tree mortality). We limited sites to northerly (315° to 45°) or southerly (135° to 225°) aspects to maximize differences in topoclimatic conditions (Kemp et al., 2016), and we limited sites to locations within 100 m of at least one live mature western larch that survived the fire and could serve as a seed source (Davis et al. 2019). Finally, potential sites were located on public lands managed by the US Forest Service, within 2 km of a road for

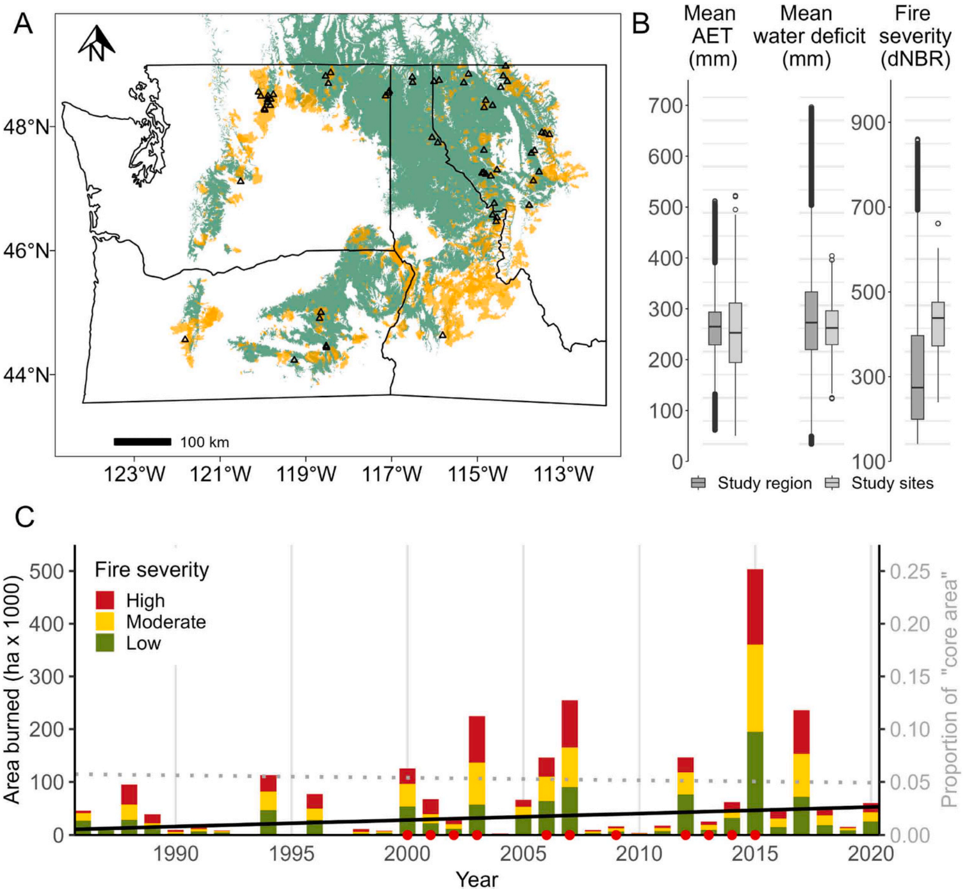

Fig. 1. Study region, site locations, and characteristic climate, fire severity and area burned for western larch in the northwestern United States ("Northwest"). (A) Map of western larch distribution (turquoise; Rehfeldt & Jaquish, 2010), study site locations (triangles) and all fire perimeters (orange polygons) of fires that overlapped with the distribution of western larch in the Northwest from 1986 to 2020. (B) Mean growing season (May-September) actual evapotranspiration (AET) and climatic water deficit from 1991 to2020 (250-m pixel resolution; Abatzoglou et al., 2018) across the distribution of western larch in the Northwest and at sample sites. Satellite-derived fire severity for all 30-m pixels of fires that burned from 1986 to 2020 across the distribution of western larch in the Northwest and range of fire severity sampled across sites within select fires from 2000 to 2015. (C) Annual burned area within the distribution of western larch in the Northwest from 1986 to2020. Colors represent proportional burn severity (dNBR); low (0–185 dNBR, green) moderate (186–417 dNBR, yellow), and high (>418 dNBR, red). Red dots represent the years that the sampled wildfires burned. Trend in annual burned area (black line; Theil-Sen's slope) is significant ($p < 0.001$) with an increase of 1150 ha·yr^{-1}. Proportion of "core area," defined as the proportion of total area burned that was > 100 m from a low-severity, moderate-severity, or unburned patch (grey line; Theil-Sen's slope) did not change significantly over time.

accessibility, and with no records of post-fire planting or salvage logging (USDA Forest Service Activity Tracking System database). We used a geographic information system to select random points that matched the above criteria and then used Garmin GPS devices to navigate to the point in the field. After verifying that the point, in fact, met the above criteria, it became the start of our belt transect for that site (see below). We sampled 57 sites from among a randomly selected set of sites meeting these criteria.

2.3. *Field sampling*

Sampling was conducted in the summers of 2021 and 2022. Each site was sampled using a 60-m long belt transect. At each site we recorded: aspect; post-fire western larch seedling density; and distance to seed source (i.e., a live, reproductively mature western larch) measured at 0, 30, a 60 m along the transect using a laser rangefinder.

We destructively sampled all western larch seedlings within the 60-m long transect, in variable widths ranging from 0.1 to 20 m (corresponding to 6–1200 m^2). Belt width varied to achieve the goal of sampling 30–40 western larch seedlings per transect (Davis et al., 2019). For destructive sampling, soil was excavated around the root collar of each juvenile, and a stem segment extending 10 cm below and 10 cm above the root collar was removed. If no juveniles were present, site data was collected with post-fire recruitment recorded as 0 for all years.

2.4. *Dendrochronology*

We used dendrochronological methods to estimate the germination year of each sample and calculate annual recruitment rates at each site. We cut samples into consecutive 2 cm segments above and below the root collar and sanded the bottom of each segment using finer-grit sandpaper (1000–2000 grit; Speer, 2010). Tree rings were counted on each sample at 10–40x magnification using a Nikon SMZ645 stereomicroscope (Nikon Instruments, Melville, New York, USA). The segment with the most rings was used to determine the germination year (Davis et al., 2019; Hankin et al., 2019; Rother & Veblen, 2016; Urza & Sibold, 2017).

To assess the precision of our age estimates, one independent researcher re-counted the tree rings of 10 % of seedlings samples. We used the mean absolute value in age discrepancy between the two counts to discern precision. We excluded 2.3 % of the samples with indistinct ring boundaries, and thus ambiguous germination dates, from the final dataset.

2.5. Statistically modeling the probability of post-fire western larch recruitment

The goal of statistical modeling was to quantify the relationship between annual climate and western larch recruitment after moderate to high severity fire. We used boosted regression trees (BRT; Elith, 2008) to model annual probability of post-fire western larch recruitment as a function of wildfire-related and climate-related variables. Specifically, we modeled the probability of recruitment in any given year as a binomial process, with "success" defined by annual recruitment rates (# juveniles $ha^{-1} \cdot yr^{-1}$) exceeding the 25th percentile of annual recruitment rates from all years with recruitment among all sites (i.e., 125 juveniles $ha^{-1} \cdot yr^{-1}$). We also investigated alternative thresholds to define recruitment (i.e., 50th percentile, 444 juveniles $ha^{-1} \cdot yr^{-1}$; presence/absence).

Dynamic predictors (i.e., time-varying) included time since fire and seasonal post-fire climate. Time since fire was the number of years between the fire event and the germination year. To represent seasonal post-fire climate, we considered several bioclimatic variables (Table 1) affecting plant-water relations and acute thermal stress impacting germination and survival (Davis et al., 2019; Kemp et al., 2016; Rank et al., 2022). Bioclimatic variables were modeled using the ECH2O ecohydrology model (Maneta & Silverman, 2013) and Topofire (Holden et al., 2016) from 1991 to 2021 at daily timescales, and then summarized to seasonal values for each recruitment year at each site following methods described by Simeone et al., (2019). Both Topofire and ECH2O output are at 30 m resolution and incorporate topo-edaphic characteristics modulating energy inputs and moisture availability.

Static predictors (i.e., non-time-varying) included wildfire-related factors found in past research to be important for post-fire conifer recruitment: fire severity and distance to seed source. Fire severity was determined using the differenced normalized burn ratio (dNBR) at 30-m pixel resolution (Parks et al., 2018). Distance to seed source was assessed in the field with a laser range finder. We used the average from among the three measurements of distance to seed source along the belt transect as a single value. Although we do not know that the individuals measured actually dispersed seeds to the areas sampled, this variable has been a significant predictor of post-fire seedling density in a number of previous studies in conifer forests (Stevens-Rumann & Morgan, 2019).

We developed BRT models using the "dismo" package and the "gbm.step" function (Hijmans et al., 2017) in R version 3.3.3 (R Core Team, 2013). We created a grid-search algorithm to construct and identify an optimized model. The algorithm used time since fire, distance to seed source, and fire severity as fixed variables. In each iteration, the algorithm assessed the impacts of adding all combinations of one energy and one moisture-related seasonal climate variable on model performance metrics. To account for the lack of spatial independence in our observations, the model-selection process incorporated spatially explicit leave-one-out cross-validation with each fire as a fold for evaluating model performance. In the case where one fire had only one class (e.g., no recruitment in any year post-fire) – which prevented calculation of performance metrics – we joined that fire with its nearest neighbor, resulting in 27 folds. We assessed performance with the AUC statistic, accuracy (the proportion of correctly classified instances out of the total instances), precision (the proportion of true positives out of the predicted positive instances), recall (the proportion of true positives out of the actual positive instances), and F-1 score (the harmonic mean of precision and recall). Each performance metric (i.e., AUC, accuracy, precision, recall, and F-1) score can range from 0 to 1, with values closer to 1 signifying better performance. Final climate predictors were selected based on these model skill metrics and how well they summarize simultaneous water and energy availability in a way that is ecologically relevant to plant distributions.

The relative influence of each variable was determined by each variable’s contribution to reduction of model deviance, as determined by the gbm.step function’s internal k-folds cross validation. We used the relative influence to assess the overall importance of varying predictor

Table 1
Predictor variables considered in the statistical model predicting annual recruitment.

Process	Variable	Units	Description
Wildfire-related	Distance to seed source	Meter (m)	Field measured (Closest live reproductive western larch). Bounded [0,100]. Continuous. Static.
	Fire severity	unitless	Satellite derived fire severity (dNBR). Sampled range [>180]. Continuous. Static. (Parks et al. 2018)
	Time since fire	Years	Derived from year of germination minus year of fire. Sampled range [1,22]. Discrete. Dynamic.
Climate	Minimum soil moisture minimum (summer)	Volumetric water content	Summer (June–August) minimum soil moisture of each recruitment year modeled at 10 cm depth and 10 % canopy cover. Volumetric water content is the ratio of the volume of water to the volume of soil. Sampled range [0.04, 0.14]. Continuous. Dynamic. (ECH2O Ecohydrology Model; Maneta & Silverman, 2013)
	Mean soil moisture (recruitment season)	Volumetric water content	April–May mean soil moisture of each recruitment year modeled at 10 cm depth and 10 % canopy cover. Volumetric water content is the ratio of the volume of water to the volume of soil. Sampled range [0.11, 0.26]. Continuous. Dynamic. (ECH2O Ecohydrology Model; Maneta & Silverman, 2013)
	Mean temperature (recruitment season)	℃	April–May mean temperature of each recruitment year. Sampled range [1,13]. Continuous. Dynamic. (Topofire; 30-m pixel resolution; Holden et al., 2016)
	Maximum surface temperature (summer)	℃	Summer (June–August) maximum surface temperature of each recruitment year modeled with 10 % canopy cover. Sampled range [31,58]. Continuous. Dynamic. (ECH2O Ecohydrology Model; Maneta & Silverman, 2013)
	Growing degree-days (temp. above 5 ℃)	℃	Cumulative growing degree-days (Jan.-Oct.) of each recruitment year; sum of degrees above 5 ℃. Sampled range[930,2180]. Continuous. Dynamic. (Topofire; Holden et al., 2016)
	Water deficit (growing season)	Millimeter (mm)	Growing season (May–Sept.) cumulative climatic water deficit of each recruitment year. Calculated as the difference between potential evapotranspiration and actual evapotranspiration. Sampled range [135,670]. Continuous. Dynamic.

(*continued on next page*)

Table 1 (*continued*)

Process	Variable	Units	Description
			(Topofire; Holden et al., 2016)
	Actual evapotranspiration (AET; growing season)	Millimeter (mm)	Growing season (May–Sept.) cumulative actual evapotranspiration of each recruitment year. Sampled range [150,415]. Continuous. Dynamic. (Topofire; Holden et al., 2016)

variables for influencing the probability of post-fire western larch regeneration.

2.6. *Climate suitability for post-fire western larch recruitment*

To investigate how the climate suitability for western larch recruitment has changed over time (1991–2021), we first assessed trends in the climate variables selected in the final model using linear mixed-effects models (LMM). We further assessed if trends over time varied between sites classified as 'warmer-and-drier' or 'cooler-and-wetter,' defined by a site's 30-yr (1991–2020) average climatic water deficit being above ('warmer-and-drier') or below ('cooler-and-wetter') the median 30-yr average climatic water deficit of all sites. We built four models of climatic trends as a function of year (1991–2021): one each for growing season actual evapotranspiration (AET) at warmer-and-drier sites combined and cooler-and-wetter sites combined, and one each for growing season water deficit at warmer-and-drier sites combined and cooler-and-wetter sites combined. Models were built with a Gaussian distribution and identity link using the R package "lme4" (Bates et al., 2014). We included site as a 'random intercept' to account for repeated measurements.

We then used the final BRT model to hindcast annual probability of post-fire recruitment across all study sites, using similar methods as Davis et al. (2019). Hindcasts were made using median distance to seed source and fire severity values observed across all study sites (i.e., 24.5 m; dNBR = 545). Seasonal climate conditions varied based on climate time series specific to each site. For each year and site combination, we made five predictions, in which time since fire varied from one to five, and then averaged those predictions to calculate mean recruitment probability in the first five years post-fire.

We tested for linear trends over time (i.e., 1991–2021) in the hindcasted annual probability of recruitment first for all sites together. We then tested for differences in the linear trends between the warmer-and-drier sites and the cooler-and-wetter sites. To assess these trends over time we built two linear mixed-effects models of recruitment probability as a function of year (1991–2021): The first model included only year as a predictor of recruitment probability, assessing for trends across all sites, whereas the second model also included average site climate (i.e., warm/dry or cool/wet) as an interaction term with the predictor 'year' to assess for trends specific to 'warmer-and-drier' or 'cooler-and-wetter' sites. Models were built with a Gaussian distribution and identity link using the R package "lme4" (Bates et al., 2014). We included site as a 'random intercept' to account for repeated measurements.

To examine the spatial variability in climate suitability for post-fire western larch recruitment, we built a second BRT model with the same predictors as the final BRT model described above, except with climate modeled at 250-m pixel resolution, that of the spatially continuous climate predictors available. We used this model to project recruitment probability across the range of western larch in the US (Rehfeldt & Jaquish, 2010, with a 1 km buffer). Distance to seed source and fire severity were set to sampled medians, as described above. We varied time since fire from 1 to 10 years, and then we presented two projections for each year, one averaging time since fire years 1–5, and a second averaging years 6–10.

3. Results

We sampled 57 sites ranging in elevation from 914 to 1943 m (mean = 1438 m) and in slope from 2 % to 60 % (mean = 28 %). Across the study sites, growing season actual evapotranspiration ranged from 98 to 407 mm (mean = 251 mm) and growing season climatic water deficit from 18 to 537 mm (mean = 242 mm; Fig. 1, 1991–2020 averages at 250-m pixel resolution; Holden et al., 2016). Sites were distributed among 37 different fires, which burned between 2000 and 2015. Fire severity at sampled sites ranged from 180 to 954 dNBR (mean = 534 dNBR; Fig. 1).

We sampled an average of 29 juveniles per site (range = 1–70; standard deviation = 14). Approximately 98 % of our total samples met our confidence criteria for age estimates. In total, we aged 1651 juvenile samples, varying in age from 1 to 22 years; this yielded 681 individual year-by-site combinations, the sample size in the BRT model. Tree ring counts were robust to validation by random, independent recounts, with germination years equal for 87 % of the samples, +/- 1 year for 12 % of the samples, and +/- $\geq$ 2 years for 1 % of samples.

The final BRT model predicted the probability of exceeding the recruitment threshold in any given year with high skill (mean AUC = 0.86; Table 2). Leave-one-out cross-validation resulted in a mean accuracy of 0.75, precision of 0.73, recall of 0.63, and F1 score of 0.66 (Table 2), indicating a reasonable balance between precision and recall.

Our model selection identified the following predictors of probability of post-fire western larch recruitment, listed in descending order of relative influence in the model: time since fire 56 %), distance to seed source (25 %), growing season actual evapotranspiration of recruitment years (7 %), satellite-derived burn severity (6 %), and growing season water deficit of recruitment years (6 %).

3.1. *Influence of wildfire-related factors on western larch recruitment*

Wildfire-related factors explained the majority of annual variability in western larch recruitment across all sites, accounting for a total of 87 % of the relative influence in the BRT model. Time since fire was the most influential variable informing the probability of recruitment, with a relative influence of 56 %. The annual probability of recruitment (i.e., >125 juveniles germinating $ha^{-1} \cdot yr^{-1}$) decreased sharply after five years, from above 0.5 in years 1–5 to below 0.1 in years 6–10. This is consistent with the observation that 87 % of western larch recruitment occurred within the first five years after a fire (Figs. 2 and 3).

Distance to seed source and fire severity were the next two most influential wildfire-related variables influencing interannual variability in western larch recruitment, accounting for 25 % and 6 % of the relative influence, respectively (cumulatively, 31 %). Annual probability of post-fire western larch recruitment exhibited a strong negative relationship with distance to seed source (Fig. 3), whereas the annual probability of recruitment exhibited a modest positive relationship with fire severity (Fig. 3). Distance to seed source was only modestly correlated with fire severity (as measured by dNBR; Spearman's rank correlation, r = 0.30, p < 0.001).

3.2. *Post-fire climate-recruitment relationships*

Growing season actual evapotranspiration and growing season water deficit during recruitment years had a relative influence of 7 % and 6 %, respectively (13 % total; Fig. 3). The annual probability of recruitment decreased as growing season water deficit increased, from c. 200 mm to 500 mm (Fig. 3). The annual probability of recruitment displayed a hump-shaped relationship with growing season actual evapotranspiration, increasing as actual evapotranspiration increased from c. 150 mm to 275 mm and subsequently decreasing from c. 275 mm to 375 mm (Fig. 3). Our results were generally robust to using alternative thresholds

Table 2

Summary statistics of model selection process.

Model predictors			**Cross-validated performance metrics**				
Energy variable	Moisture variable	Fixed vars.	AUC (sd)	Acc. (sd)	Prec. (sd)	Recall (sd)	F1-score (sd)
–	–	tsf	0.82 (0.15)	0.73 (0.13)	0.66 (0.28)	0.74 (0.19)	0.64 (0.19)
–	–	tsf, dss	0.84 (0.15)	0.72 (0.16)	0.69 (0.28)	0.59 (0.36)	0.65 (0.21)
–	–	tsf, dss, dnbr	0.88 (0.12)	0.74 (0.15)	0.72 (0.28)	0.64 (0.32)	0.65 (0.18)
Water deficit (gs)	Soil moist. mean (rs)	tsf, dss, dnbr	0.87 (0.12)	0.74 (0.17)	0.73 (0.28)	0.64 (0.30)	0.66 (0.19)
Water deficit (gs)	**AET (gs)**	**tsf, dss, dnbr**	**0.86 (0.11)**	**0.75 (0.17)**	**0.73 (0.27)**	**0.63 (0.32)**	**0.66 (0.21)**
Water deficit (gs)	Soil moist. min. (summer)	tsf, dss, dnbr	0.86 (0.13)	0.73 (0.17)	0.70 (0.27)	0.64 (0.33)	0.62 (0.23)
GDD > 5 °C	Soil moist. min. (summer)	tsf, dss, dnbr	0.86 (0.13)	0.73 (0.17)	0.72 (0.28)	0.63 (0.30)	0.65 (0.18)
Surface temp. max. (summer)	Soil moist. mean (rs)	tsf, dss, dnbr	0.85 (0.131)	0.74 (0.16)	0.74 (0.28)	0.61 (0.31)	0.64 (0.21)
Surface temp. max. (summer)	Soil moist. min. (summer)	tsf, dss, dnbr	0.85 (0.14)	0.73 (0.16)	0.73 (0.27)	0.62 (0.32)	0.63 (0.21)
Surface temp. max. (summer)	AET (gs)	tsf, dss, dnbr	0.84 (0.13)	0.74 (0.14)	0.73 (0.28)	0.63 (0.30)	0.65 (0.17)
GDD > 5 °C	Soil moist. mean (rs)	tsf, dss, dnbr	0.86 (0.13)	0.73 (0.17)	0.72 (0.29)	0.62 (0.29)	0.65 (0.19)
Temp. mean. (rs)	Soil moist. mean (rs)	tsf, dss, dnbr	0.86 (0.12)	0.73 (0.15)	0.72 (0.31)	0.62 (0.30)	0.62 (0.22)
GDD > 5 °C	AET (gs)	tsf, dss, dnbr	0.85 (0.14)	0.71 (0.16)	0.69 (0.29)	0.60 (0.29)	0.62 (0.18)
Temp. mean. (rs)	Soil moist. min. (summer)	tsf, dss, dnbr	0.84 (0.15)	0.73 (0.15)	0.71 (0.26)	0.66 (0.29)	0.60 (0.21)
Temp. mean. (rs)	AET (gs)	tsf, dss, dnbr	0.84 (0.13)	0.72 (0.15)	0.69 (0.27)	0.62 (0.32)	0.63 (0.20)

* Bold text refers to the combination of variables selected for the final model.

** AUC = Area Under the receiver-operator Curve; Acc. = accuracy; Prec. = precision

*** gs = growing season; rs = recruitment season (see Table 1)

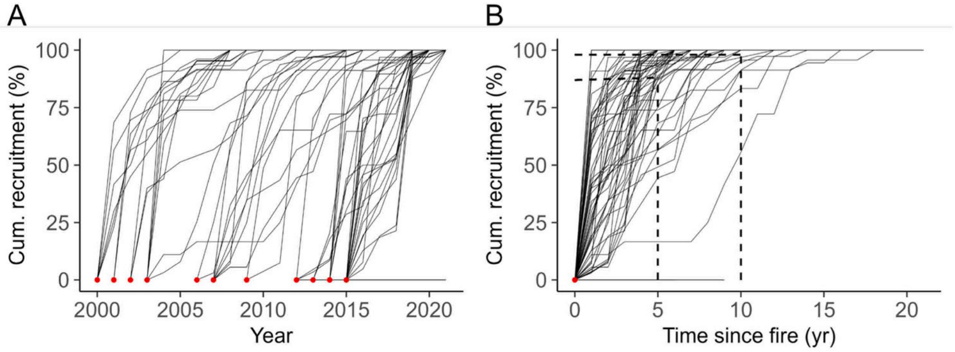

Fig. 2. Cumulative recruitment following fires for each of the 57 sites sampled. (A) Recruitment by calendar year, and (B) recruitment by time-since-fire. The black dashed lines at time-since-fire of 5 and 10 years corresponds to the average cumulative recruitment among sites of 87 % and 98 %, respectively. Red dots represent fire years of fires sampled.

to define recruitment (i.e., presence/absence, $\geq$ 1 juvenile establishing $ha^{-1}\cdot yr^{-1}$; 50th percentile, 444 juveniles establishing $ha^{-1}\cdot yr^{-1}$; Fig. A.1 and A.2).

Results from the BRT model highlighting the influence of growing season climate were consistent with patterns observed in the overall dataset. Post-fire western larch recruitment was significantly higher at sites with northerly compared to southerly aspects (Pearson's Chi-squared test; $\chi^2 = 72.6$, df = 1, $p < 0.001$, n= 240; Fig. A.3). This corresponded to differences in growing season water deficit, which was significantly higher during years of recruitment at sites with southerly aspects (mean = 375.9 mm, standard deviation = 100.6 mm) compared to years of recruitment at sites with northerly aspects (mean = 334.6 mm, standard deviation = 91.9; Mann-Whitney U test, W = 61517, $p < 0.001$, n = 681; Fig. A.3). Growing season actual evapotranspiration during the recruitment year was not significantly different between sites with northerly and southerly aspects (Mann-Whitney U test, W = 47859, $p > 0.05$, n = 681; Fig. A.3).

3.3. *Spatial and temporal variability in the climate suitability for post-fire recruitment*

Growing season actual evapotranspiration decreased significantly over time (cooler-and-wetter sites: n = 28, slope [SE] = -2.2 mm/yr [0.1337], T = -16.34, $p < 0.001$; warmer-and-drier sites: n = 29, slope [SE] = -2.3 mm/yr [0.1487], T = -15.18, $p < 0.001$; Fig. 4), and growing season climatic water deficit increased significantly over time (cooler-and-wetter sites: n = 28, slope [SE] = 4.0 mm/yr [0.2884], T = 13.91, $p < 0.001$; warmer-and-drier sites: n = 29, slope [SE] = 3.3 mm/yr [0.2893], T = 11.44, $p < 0.001$; Fig. 4). Despite these directional trends in climate from 1991–2021, there was no statistically significant trend in recruitment probability over time when modeling all sites together. When we added average site climate and its interaction with year to the model, there was a modest but statistically significant increase in recruitment probability over time at cooler-and-wetter sites (slope[SE] = 0.0007/yr [0.0001], $p < 0.001$, Fig. 4) and a modest but significant decrease over time at warmer-and-drier sites (slope[SE] = -0.0004/yr [0.0001], p = 0.006, Fig. 4). Overall, between 1991 and 2021, recruitment probability at cooler-and-drier sites increased slightly (0.021), whereas recruitment probability at warmer-and-drier sites decreased slightly (-0.012).

Across the range of western larch in the Northwest, the probability of post-fire western larch recruitment was generally high for the first 5 years after fire (0.51–0.78), dropping below 0.39 from 6 to 10 years post-fire (Fig. 5). Regionally, climatic suitability was consistently highest in upper montane areas of the Eastern Cascades (WA), Columbia Rockies (WA), Kootenai Mountains (ID), Bitterroot Mountains (MT), and Blue Mountains (WA/OR; Fig. 5).

4. Discussion

Western larch regeneration was more sensitive to wildfire-related factors than to seasonal climate conditions (Fig. 3). Variability in seedling recruitment rates was largely explained by time since fire and distance to the nearest live mature western larch, which likely served as a

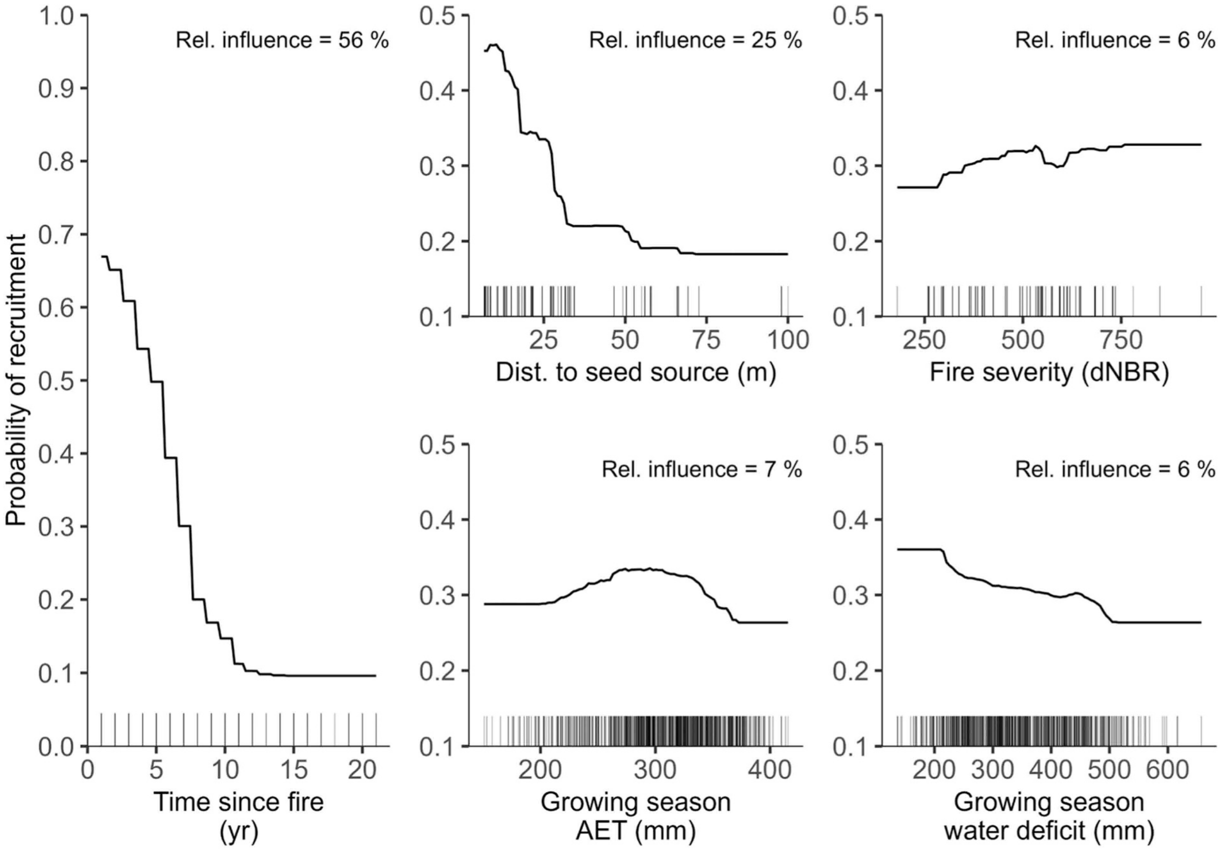

Fig. 3. Partial dependence plots for the five most important variables predicting post-fire recruitment of western larch, defined using a recruitment threshold of 125 juveniles $ha^{-1}·yr^{-1}$ (i.e., the 25th percentile of recruitment rates for years with recruitment across plots). Marginal effects of wildfire-related variables (time since fire, distance to seed source, fire severity) and climate variables (growing season actual evapotranspiration [AET] and climatic water deficit of the recruitment year; 30-m pixel resolution) on annual recruitment probability, after accounting for the average effects of all other variables in the model. Relative influence of each variable, determined by each variable's contribution to the reduction in variance in the model, is reported in the upper-right of each plot.

seed source. Fire severity had a modest positive influence on post-fire regeneration. After accounting for wildfire-related factors, climate also had a modest influence on post-fire regeneration, with a lower probability of recruitment during years with warmer and drier conditions and high actual evapotranspiration. The influence of aspect, which was strongly tied to spatial variability in growing season water deficit was also apparent, with higher recruitment probability on northerly aspects (Fig. A.3).

Directional changes in growing season water deficit and actual evapotranspiration have resulted in slightly increased climatic suitability for western larch regeneration at cooler-and-wetter sites and slightly decreased climatic suitability at warmer-and-drier sites (Fig. 4). Our findings suggest that management goals to support western larch in future forests are consistent with, and would likely benefit from, moderate- and high-severity fires that burn with spatial heterogeneity.

4.1. Influence of wildfire-related factors on post-fire regeneration

The regeneration of western larch after wildfires was more strongly related to fire-related variables than seasonal climate conditions. In our statistical model, the relative influence of time since fire alone (56 %) was more than four times the combined influence of seasonal post-fire climate variables (13 %, Fig. 3). Further, 87 % of all post-fire recruitment occurred within five years following wildfires (Fig. 2), highlighting wildfire itself as a dominant factor determining regeneration. This is consistent with previous research highlighting higher western larch seed germination on post-fire residual duff layers less than 1.25 cm thick, relative to thicker duff layers or unburned soils, and high seedling vigor when competing vegetation was removed by high-intensity wildfire (Debyle and Norbert, 1981; Gower and Richards, 1990). Opportunities for western larch establishment diminish rapidly after wildfire, due to the decline of early seral stand conditions, including high availability of mineral soil seed beds and low canopy cover. Sites that burned with higher fire severity also had a higher probability of western larch recruitment, compared to sites that burned at lower severity, consistent with most recent studies (Hoecker & Turner, 2022; Urza & Sibold, 2017; although see Povak et al. 2020) and the importance of early seral conditions for this shade-intolerant species (Fiedler & Lloyd, 1995; Schmidt et al., 1976; Schmidt & Shearer, 1995).

The distance to surviving trees that can serve as a post-fire seed source ('distance to seed source'), in part determined by the size of patches burned at high severity (e.g., Harvey et al., 2016; Kemp et al., 2016), was also an important predictor of western larch recruitment. Recruitment probability decreased substantially with increasing distance to seed source. This result is consistent with numerous previous studies with multiple non-serotinus conifer species across western North America (Harvey et al., 2016; Kemp et al., 2016; Peeler & Smithwick, 2020; Povak et al., 2020; Stevens-Rumann et al., 2018; Urza & Sibold, 2017).

4.2. Influence of growing season climate on post-fire regeneration

Post-fire climate conditions had a significant but modest influence on the regeneration of western larch after wildfires. Western larch recruitment probability decreased with increased growing season climatic water deficit and showed a hump-shaped relationship with growing season actual evapotranspiration during recruitment years. Decreased recruitment with increased growing season climatic water

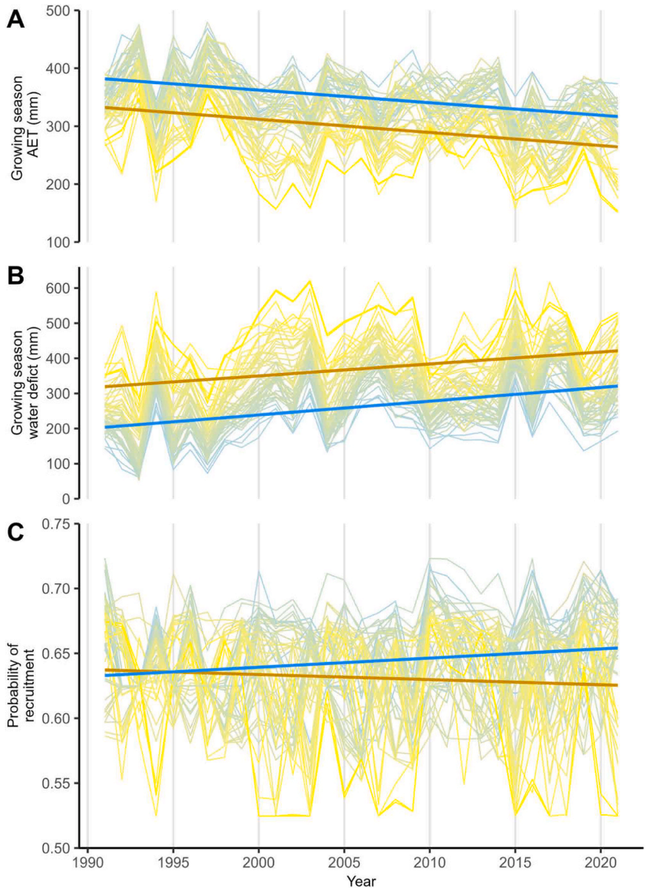

Fig. 4. Time series of the most influential climate variables affecting the probability of post-fire western larch recruitment and overall climate suitability for western larch recruitment in the Northwest. (A) Growing season actual evapotranspiration (AET) decreased, and (B) growing season climatic water deficit increased over the 1991–2021 period in both warmer and drier sites (thick brown lines) and cooler and wetter sites (thick blue lines). (C) Average probability of recruitment – "climate suitability" – decreased significantly but modestly over time at warmer and drier sites (thick brown line) and increased significantly but modestly at cooler and wetter sites (thick blue line). Thin lines represent individual sites and are colored to reflect site-specific 30-yr mean growing season climatic water deficit (1991–2020), from low (blue) to high (yellow). The probability of recruitment reflects the average predictions across years 1–5 after wildfire, while holding constant distance to seed source (24.5 m) and fire severity (dNBR 545) at their median values.

deficit is consistent with the mechanism of increased water stress limiting conifer establishment and survival (Miller & Johnson, 2017; Sapes et al., 2019; Schmidt et al., 1976; Simeone et al., 2019). The influence of growing season actual evapotranspiration is also consistent with this mechanism, for values under c. 275 mm: increased actual evapotranspiration was associated with a higher probability of recruitment. When actual evapotranspiration exceeded c. 275 mm, however, recruitment probability decreased. This decrease may reflect competition from other vegetation (Franklin et al., 2002; Oliver & Larson, 1996; Stephenson, 1990) under more productive conditions (in space and/or time). For example, competition for light could limit the recruitment of highly shade-intolerant western larch (Cole & Schmidt, 1986; Fiedler et al., 1995). Overall, our results indicate that climate suitability for post-fire recruitment is highest during years with low water deficit and near-average actual evapotranspiration (Figs. 3 and 5).

In other regionally specific studies, the impacts of warm and dry climate conditions on post-fire western larch regeneration have been mixed. Two studies in Glacier National Park (MT) did not detect a relationship between post-fire drought and density of post-fire western larch regeneration (Harvey et al., 2016; Hoecker & Turner, 2022). Other studies, in Glacier National Park (Urza & Sibold, 2017) and the Blue Mountains (WA; Andrus et al., 2022), estimated tree ages with non-destructive methods and found western larch seedling establishment was higher with wetter post-fire climatic conditions. Another study in the Okanogan Mountains (WA) found lower western larch regeneration at sites characterized by higher mean annual temperature, yet regeneration did not vary with differences in mean annual precipitation (Povak, et al., 2020). In a broader geographic study, yet still limited to Idaho and Montana, Steed & Goeking (2020) found the highest suitability for western larch recruitment within the cooler and drier portions of their study region. None of these studies examined post-fire western larch recruitment across its climatic range in the United States, and many used a space-for-time substitution to evaluate climate impacts, likely explaining the contrasting results. Our study helps clarify some of the variability among prior work, by comparing annual post-fire recruitment to seasonal climate conditions, across the climatic range of western larch in the United States.

4.3. *Spatial and temporal variability in the climate suitability for post-fire regeneration*

Growing season climatic water deficit has increased significantly, while actual evapotranspiration has decreased significantly over the study sites in recent decades (i.e., 1991–2021; Fig. 4). The combined impacts of these changes – each of which could have varying effects – resulted in no significant change in the overall probability of post-fire western larch recruitment across all sites combined (i.e., 'climate suitability'; Fig. 4). However, separating sites by average climate conditions revealed modest increases in the climate suitability for post-fire recruitment among cooler-and-wetter sites, and modest decreases in climate suitability for among warmer-and-drier sites (Fig. 4). Thus, recent climate change has had small yet detectable impacts on the climate suitability for post-fire western larch regeneration across its range in the United States.

Our results demonstrating overall high climate suitability for post-fire regeneration of western larch over recent decades are consistent with findings for several other conifers in montane and subalpine forests of the Northern Rockies and Interior Northwest, including *Pinus contorta*, *Picea engelmannii*, and *Abies* spp. (Davis et al., 2023; Littlefield, 2019; Povak et al., 2020; Wolf et al., 2021). In contrast, climate conditions have become increasingly unsuitable for post-fire regeneration of two widespread conifers, ponderosa pine and Douglas-fir, specifically in the warmest and driest portions of their ranges (i.e., low-elevation forests and southern extents; Davis et al., 2019; Rodman et al., 2020). Although we also detected a slight decline in climate suitability for western larch among warmer-and-drier sites, overall climate suitability remained high in recent decades.

The varying impacts of growing season actual evapotranspiration (AET) and water deficit revealed in our study have important implications for anticipating future changes in the climate suitability for post-fire recruitment of western larch. Over recent decades growing season AET among our cooler-and-wetter sites was generally above c. 275 mm, where decreasing AET is associated with increasing recruitment probability (Fig. 3). Conversely, at warmer-and-drier sites, growing season AET was generally below c. 275 mm, where decreasing AET is associated with lower recruitment probability (Fig. 3). As a result, decreasing growing season AET in recent decades contributed to increasing recruitment probability in cooler-and-wetter sites, offsetting the effect of increasing growing season climatic water deficit (Fig. 4). Yet in warmer-and-drier sites decreased AET compounded the increase in water deficit, resulting in declining recruitment probability. Therefore, although climate suitability for post-fire western larch regeneration is shifting within the distribution of western larch in the United States, there is a net-neutral effect on the likelihood of regeneration (Fig. 4). If the trend of decreasing growing season AET continues, AET at the cooler-and-

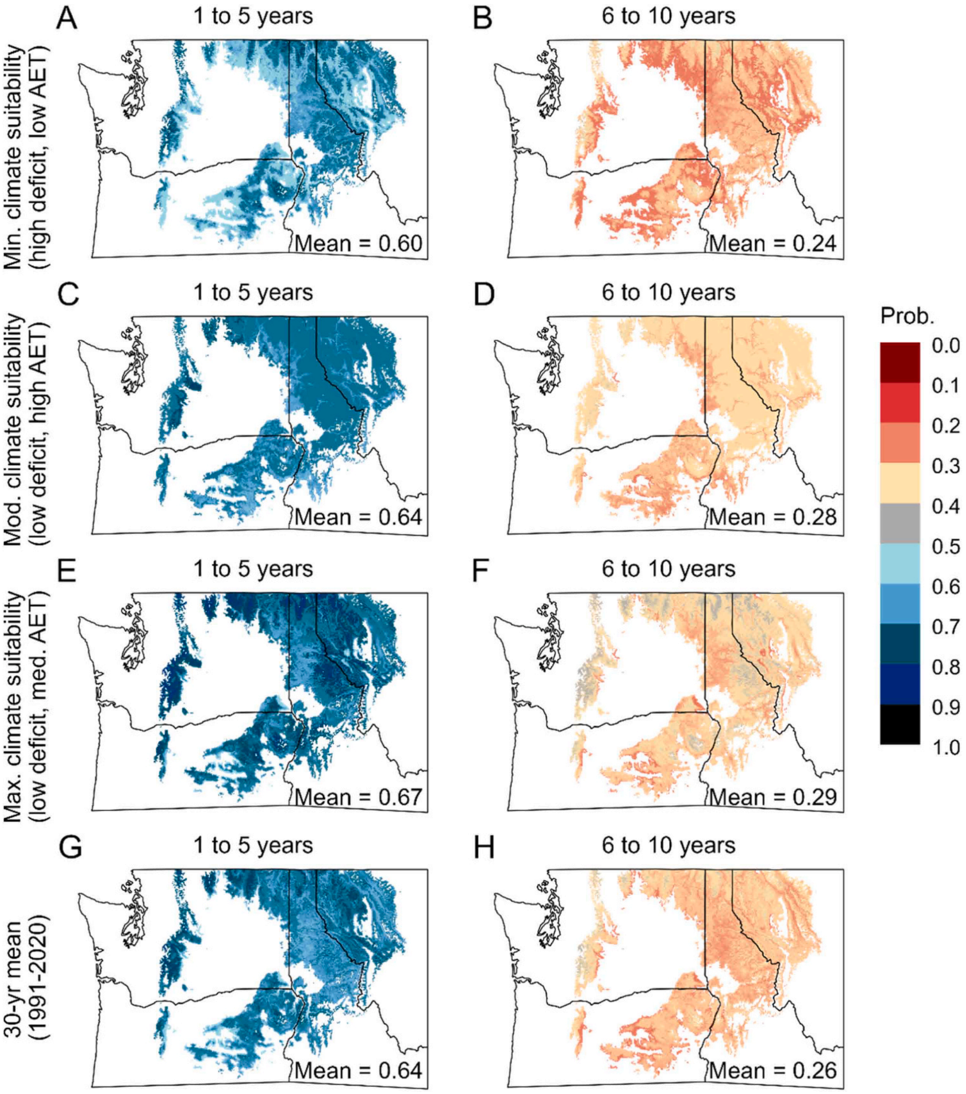

Fig. 5. Climate suitability for post-fire western larch recruitment for four example years (A-F) and for the average climate conditions over the 1991–2020 period (G-H) across the distribution of western larch (+ 1 km buffer). Recruitment probability was averaged across two post-fire time periods, years 1–5 (left column) and years 6–10 (right column). Example years highlight varying combinations of water deficit and AET between 1991 and 2020: high deficit, low AET (A, B; 2015); low deficit, high AET (C, D; 1997); low deficit, median ("med.") AET (E, F; 2010); and the 30-year mean from 1991 to 2020 (G, H; 1991–2020). For all climate scenarios recruitment probability ranged from 0.51 to 0.78 1–5 years after fire and 0.19–0.39 6–10 years after fire. The probability of recruitment was estimated while holding distance to seed source and fire severity constant at their median values (i.e., 24.5 m and dNBR of 545). "Max." is maximum, "mod." is moderate, and "min." is minimum.

wetter sites will eventually drop below c. 275 mm, and continued declines would then contribute to, rather than negate, the effects of increased water deficit on post-fire regeneration at these sites.

These complex impacts of changing AET on the climate suitability for post-fire western larch regeneration may help explain, in part, widely varying projections of changing climate suitability for mature western larch, unrelated to post-fire regeneration. Rehfeldt and Jaquish (2010) developed bioclimatic models for mature western larch across its entire range, and then informed those models with climate projections from a range of general circulation models; the geographic range of mature western larch was projected to decrease by anywhere from 1 to 99 percent by 2090.

4.4. *Implication for future forests and forest management*

Our study has three important implications for forest management activities aimed at maintaining western larch as a component of future forests. First, efforts to generate spatially heterogeneous burning with moderate- and high-severity patches (Hessburg, 2016; Hopkins et al., 2014) will likely create more opportunities for western larch recruitment, so long as area within high severity patches are still near a potential seed source (i.e., < 100 m; Marcoux et al., 2015, Berkey et al., 2021). Our results also suggest that increased area burned in recent decades (Fig. 1; Parks & Abatzoglou, 2020), including the proportion burned at moderate severity (Fig. 1), would have been favorable for western larch regeneration by providing more early seral stand conditions and opportunities for recruitment (Hoecker & Turner, 2022; Steed & Goeking, 2020).

Second, our results provide support for current forest management practices that focus post-fire regeneration efforts on the first five years after wildfire, which we and others have found to be particularly important for western larch germination and survival (Fiedler & Lloyd, 1995; Schmidt et al., 1976). Although increased area burned has yet to significantly limit seed availability from mature western larch (Fig. 1), this is expected to change with continued increases in area burned at high severity – which implies increases in areas with long distances to live seed sources (Cansler and McKenzie, 2014; Parks & Abatzoglou, 2020). In the near term, climate remains generally suitable for western larch regeneration: between 1991 and 2021, the probability of recruitment was consistently >50 % over post-fire years 1–5, when seed source was not limiting. This implies that planting seedlings will likely be a successful strategy to maintain western larch in large, severely burned patches that supported western larch pre-fire. Planting is also an excellent tool to implement both the 'Resist' and 'Direct' approaches to climate adaptation in post-fire ecosystems (Schuurman et al., 2022; Larson et al., 2022). Planting western larch in warmer and drier portions of its range, for example, is a way to maintain western larch, 'resisting' reductions in the regeneration niche due to climate change (Fig. 4). Planting western larch in burned areas in the cooler and wetter portions of its range could help 'direct' post-fire forest community composition, facilitating recruitment and expanding the regeneration niche.

Finally, our results suggest that ongoing climate change has thus far had minimal impacts on western larch recruitment, giving managers time to consider management actions for when more substantial climate-change impacts emerge, as suggested by existing studies (Crotteau et al., 2019; Hopkins et al., 2014; Rehfeldt & Jaquish, 2010). Therefore, in a world where managers increasingly must prioritize among multiple objectives related to climate adaptation and maintaining forest resilience, western larch appears to be less immediately vulnerable to climate-change impacts than other species and forest types in the warmest and driest portions of western North America (Davis et al., 2019, 2023; Rodman et al., 2020).

CRediT authorship contribution statement

Andrew J. Larson: Writing – review & editing. **Philip E. Higuera:** Writing – review & editing, Methodology, Conceptualization. **Spencer T. Vieira:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Kimberley T. Davis:** Writing – review & editing, Methodology, Conceptualization. **Zachary A. Holden:** Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data and code used in this study are publicly available via the Dryad Data Repository: https://doi.org/10.5061/dryad.0k6djhb6r.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122011.

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