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Avery Hill (✉ aph82@stanford.edu)

Stanford University <https://orcid.org/0000-0001-7476-0107>

Christopher Field

Stanford University <https://orcid.org/0000-0002-1684-8247>

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How Competition and Wildfire Affect Tree Range Shifts in the American West

Avery P. Hill^{1*} and Christopher B. Field^{1,2}

¹Department of Biology, Stanford University, Stanford, CA, USA

²Woods Institute for the Environment, Stanford University, Stanford, CA, USA

* Correspondence

Avery Hill

aph82@stanford.edu

Abstract

Due to climate change, plant populations experience environmental conditions to which they are not adapted. Our understanding of the next century's vegetation geography depends on the distance, direction, and rate at which plants redistribute in response to a changing climate. Although plant redistribution in response to contemporary climate change is widely observed, our understanding of its mechanics is nascent. In this study we test the response of plant range shift rates to wildfire occurrence using 33,838 Forest Inventory Analysis plots across five states in the western United States. Wildfire increased the rate of observed range shifts for 6/8 tree species by more than 22% on average, suggesting that incumbent vegetation can act as a barrier to plant range shifts and that fire management may play an important role in facilitating transitions between vegetation types in response to climate change.

Main

At the broadest scale, plant biogeography is determined by climate^{1,2}. A panoply of research has supported the expectation that plant distributions should change in response to climate changes^{3–7}. Range shifts over the last century have been observed at a global scale, particularly in mountainous areas⁸, with mounting evidence of changing distributions in flatter landscapes as well^{7,9,10}. The required rates of plant range shifts (RS) to keep up with the velocity of climate change are large, relative to observed RS rates¹¹. Though these rates are highly variable between taxa, a global synthesis found that plant distributions have been shifting to higher elevations at an average rate of 1.5 m/y⁷. Of the plants that *do* track climate change—many do not^{9,12}—some have argued that RS rates are not fast enough for many species to keep pace with the velocity of climate change under contemporary conditions^{13–15}. Furthermore, plants must contend with other anthropogenic factors such as land-use change (e.g. logging, urbanization) or invasive species, which can exacerbate the vulnerability of plant populations.

Our ability to understand and predict the distribution of vegetation in the Anthropocene is important for resource management, conservation, and other efforts to secure a sustainable future. The interspecific variability and context specificity of RS rates makes modeling RS difficult. Research into the causes and ecological implications of variable RS rates is ongoing and incomplete. Features that affect the RS rate of a species include species characteristics (morphology, dispersal mechanisms, etc.), landscape characteristics (suitable habitat availability, disturbance regimes, geographic barriers), and biotic interactions (interspecific competition, predation, mutualism)¹⁶. Of these, effects of biotic interactions may be the most difficult to understand and predict— not for lack of effort¹⁷— but in part due to the specificity, conditionality, and complexity of the relationship between species interactions and local

population establishment and growth. While biotic interactions have both inhibited and facilitated RS during historical deglaciation events^{18,19}, empirical evidence of their role in contemporary RS is sparse.

Competition is known to affect range limits^{20,21}. A hypothesis that the leading edge of migrating populations may be slowed by competition with pre-existing vegetation^{16,22} is supported by some vegetation models^{23–26}. However, empirical evidence of competition slowing leading-edge RS in contemporary systems under climate change is scant²². Though some recent experimental work suggests that interspecific competition is more significant at the trailing-edge than the leading-edge in montane plant communities^{27,28}, a continental-scale and/or observational investigation into this phenomenon has not yet been conducted.

Wildfire, because it alters the intensity of competition, provides a promising avenue for studying the effects of competition on RS rate. Recent modeling indicates that disturbance has the potential to facilitate RS^{23,29–31}, specifically forest fires²⁶, by reducing competitor population size and creating clearings for colonization. Some studies show that fires can also facilitate transitions to alternative stable states, but this is not the same thing as facilitating RS due to climate change. As a cause of significant mortality, fire could have the potential to remove or thin trailing-edge populations and make room for the leading-edge of other migrating plant populations. Competition is not the only potentially range-limiting factor affected by wildfire—others include soil characteristics like nutrient composition and infiltration³². Interspecific differences in fire-adaptation and ruderal characteristics could also complicate the relationship between wildfire and competition. Fires are likely to favor fire-adapted and early-successional species shortly after burning, whether these species are immigrants or incumbents. Without empirical evidence, it is unclear how forest fires impact RS patterns.

In this study we used observational evidence from the USDA Forest Inventory and Analysis (FIA) to test the hypothesis that forest fires facilitate plant RS in response to contemporary climate change. We used all FIA plots (33,838 total) within the Northwestern Forested Mountains and Marine West Coast Forest ecoregions of the continental U.S. in a natural experiment, with historic wildfires as the treatment and observed tree RS rate as the response. We focused on RS through climate space rather than geographic space and define the source population as composed of plots with both trees and seedlings present and the leading edge (not necessarily the geographic extent of the species) as composed of plots with only seedlings present. We performed additional analysis to strengthen confidence in our characterization of each species RS direction and magnitude (including testing the possibility of sink populations at the leading edge), then compared RS rates between plots that had and had not burned in the last 5 years. Here, we show that the ranges of six tree species shifted faster through climate space in plots with a recent fire.

Results

Evidence of RS in Unburned Plots

Of the 79 tree species within the study area (Figure 1), 12 were sufficiently abundant to meet the minimum plot-level sample size for groups of both burned (B) and non-burned (N) plots and for both seedlings only (S) and trees and seedlings (T). Three of the twelve (*Picea engelmannii*, *Pinus monticola*, and *Larix occidentalis*) were filtered out due to inconsistency in the direction of RS through climate space between different life stages, and *Pinus albicaulis* was excluded due to directional inconsistency in RS between burned and unburned plots—the remaining eight are described in Table 1. Evidence of RS was strong for these eight tree species

in the unburned (control) plots: the leading-edge populations (NS, see methods) grew in significantly different climates than source populations (NT). Schoener's D is a metric of climatic niche equivalency, where values closer to 1 indicate more niche similarity, and values closer to 0 indicate less. In unburned plots, the overlap between the climatic niche of the leading edge (NS) and the source population (NT) yielded Schoener's D values from 0.82 to 0.56 (Table 2). All values of Schoener's D for unburned plots were less than 0.82 ($p < .05$), and we rejected the *niche equivalency test*'s null hypothesis that the climatic niche of the leading edge (NS) was equivalent to the niche of the source population (NT).

The climatic niche differences between leading-edge and source populations were corroborated by PCA and the Euclidean centroid distance. For example, *Pinus ponderosa* exhibited differential clustering of component scores when grouped into leading-edge and source population occurrences in unburned plots (Figure 2). Though the climatic niches of NS and NT were broadly overlapping, the centroids (the average component score coordinates) of the groups differed. The Hotelling's T^2 test, used to test the statistical significance of the difference between the centroids of two populations³³, showed that the difference between the NS and NT centroids was significant for each species (Table 2).

Comparing RS Rates of Burned and Unburned Plots

We used two metrics to compare the RS rate of burned plots and unburned plots: Euclidean centroid distance (i.e. niche distance) and Schoener's D (i.e. niche equivalency). We calculated RS Euclidean distance in climate space (DC) based on centroids with respect to three climatic variables: Mean Temperature of the Warmest Month (MTWM), Mean Summer Precipitation (MSP), Mean Winter Precipitation (MWP). The ratio of RS distance in burned to unburned plots (DC_B/DC_N , where B = burned, N = unburned) is a measure of the effect of fire

on RS rate. Based on DC_B/DC_N , the climatic niche difference between source populations and leading-edge populations was greater in areas that burned than in those that did not for six of the eight species. DC_B/DC_N was, on average, 2.10. By this metric, fire most increased the rate of RS for *Lithocarpus densiflorus*, which had the greatest ratio— 6.35 (though sample size was smallest for this species). *Abies grandis* was the only species where DC_B was appreciably less than DC_N : $DC_B/DC_N = 0.70$. The second measure of RS rate, Schoener's D, was closer to 0 (indicating less niche equivalency) for burned plots across each of the eight species, by 22% on average (Table 2). Schoener's D corroborated DC_B/DC_N for *Lithocarpus densiflorus*, which had a burned-plot Schoener's D 36% closer to 0 than in unburned plots (the greatest difference in Schoener's D across species).

With the RS broken down into each climate variable we found that RS with respect to each of the three components of the climate space was greater in plots that burned than in plots that did not, on average across the eight species (Figure 3). For example, as each species in unburned areas migrated towards plots with either higher or lower Mean Summer Precipitation (MSP), species in burned plots migrated in the same direction (either higher or lower MSP) at a rate that was 100% greater on average (Appendix 1, Fig. A1.1-A1.8). The difference between RS rates was greatest for Mean Winter Precipitation (MWP), where the average RS rate was 208% greater in burned plots. Mean Temperature of the Warmest Month (MTWM) had the least difference between RS rates, but burned plots still had an average RS rate 55% greater than unburned plots for this variable. The range of RS rates across species was greater in burned plots (Figure 3), probably reflecting the smaller sample size of burned plots.

Contextualizing the Direction of RS

When compared to recent climate change in the study area (Figure 4), the eight species, on average, shifted in the direction that kept them closer to their historic climatic niche. For example, as plots across this study received less MSP, the species shifted towards plots with more summer precipitation— with burned areas exhibiting faster RS than unburned areas (Figure 3a). Individual species varied in the extent to which their RS directly opposed climate changes across their individual distributions. Mean Summer Precipitation elicited the most consistent response— six of eight species (all but the two subalpine species, *Abies lasiocarpa* and *Pinus contorta*) shifted towards plots with greater mean summer precipitation (Appendix 1).

Based on responses to recent climatic shifts across the study area, species fall into three groups, depending on whether they (1) migrated to oppose recent climatic shifts across all three climate variables, (2) migrated to oppose recent climate shifts across one or two climate variables, or (3) migrated in the **same** direction as climate shifts for one or more variable. *Pinus ponderosa*, *Populus tremuloides*, *Quercus chrysolepis*, and *Abies grandis* fell into the first group. Additionally, the burned-plot samples for *P. ponderosa* and *P. tremuloides* exhibited faster rates of RS for each variable (Appendix 1, Fig. A1.2-A1.5). These two species had high agreement between RS vectors through the three dimensions of climate space ($\geq 93\%$) in burned and unburned plots (Table 1). Group 2 was composed of *Pseudotsuga menziesii* and *Lithocarpus densiflorus*. *P. menziesii* exhibited faster RS towards lower MTWM and higher MSP while *L. densiflorus* exhibited faster RS towards higher MSP and MWP (Appendix 1, Fig. A1.1 and A1.6). *Abies lasiocarpa* and *Pinus contorta* fell into group 3— each migrated with recent climate shifts, towards higher MTWM and lower MSP (Appendix 1, Fig. A1.7-A1.8).

Discussion

Our results are consistent with the hypothesis that forest fires facilitate climate-induced range shifts and provides some of the first empirical evidence of contemporary climate-induced RS being facilitated by fire. These findings are consistent with current understandings of range shifts, climate change, and disturbance ecology, and the observed increase in RS rate in burned areas provides insight into the role of interspecific competition in limiting RS rate.

Range edges are dynamic over time, expanding or contracting as the relationship between a population and its environment changes, because of changes in either (1) the environment (e.g. warmer temperatures, increased disturbance, etc.) and/or (2) the population (e.g. phenotypic changes in temperature tolerance, water-use efficiency, etc.). At time scales (1 to 2 generations) where evolution is unlikely to have made populations tolerant to observed climate changes, we observed range expansions where environmental variables that limit species ranges were lessened/removed. As a possible range-limiting factor for many species, interspecific competition could limit range shifts when competitors are abundant. Removal or extirpation of competitor populations could facilitate range shifts. Many types of environmental disturbance can decrease the population size of plant competitors, but none are as common and severe in western North America as wildfire.

Wildfire typically facilitates shifts in species composition along trajectories of ecological succession^{34,35}, with post-fire assemblages that are abundant shortly after fire eventually succeeded by climax vegetation. Post-fire succession can be predictable and specific to ecosystems and return an ecosystem to the initial pre-fire or climax species assemblage. In contrast, fire can also facilitate state-shifts where the post-fire trajectory of vegetation succession leads to a different suite of climax species. This kind of state shift occurs in the boreal forests of

Alaska, where fire decreases ecosystem resilience, i.e. the ability of an ecosystem to return to the initial species composition after disturbance. The observed state shifts were largely attributed to the effect of fire on species regeneration (e.g. seedbanks)^{36,37}. Fire and climate change, in concert, can affect tree regeneration further south as well, in *P. ponderosa* and *P. menziesii* forests, with warmer temperatures unsuitable for conifer seedlings that emerged after fire³⁸.

Fire could also facilitate range shifts through reducing population size and density of plant species present before the fires, increasing light availability, increasing erosion, and altering soil nutrients and microbiota³⁹— the exact impacts are contingent upon the intensity of fire as well as particular plot conditions. While plant mortality, erosion, and post-fire light availability are positively correlated with fire intensity, the relationship between fire intensity and other soil characteristics can be more complicated. In vastly simplified terms, lower intensity fires more consistently increase soil microbial activity and the availability of soil nutrients like carbon, nitrogen, sulfur, and phosphorus, while higher intensity fires can sterilize soil and deplete nutrients⁴⁰.

Most fires across our study plots were of low intensity. When possible, FIA data collectors classified fires as either crown or ground fires. Ground fires, typically of lower intensity than crown fires⁴¹, composed 63% of the fires cited across the FIA plots of this study. This suggests that most fires within this study increased soil nutrients and microbial activity while moderately increasing light availability and erosion. While the high intensity fires (with subsequent soil sterilization and nutrient depletion) and increased erosion could have presented challenges for seedling establishment, most of the wildfires presumably increased establishment rate across the study area due to an increase in soil nutrients and reduction in interspecific competitors for light and water.

In accordance with basic ecological theory, where resources are more abundant (like light and nutrients) and competitors fewer, populations grow. Unless species have particular adaptations for post-fire regeneration (fire-induced seed release or re-sprouting), population growth is accomplished by recolonization from nearby populations. A gap in the canopy, or a spot cleared of underbrush with sufficient available nutrients, welcomes the establishment of vegetation. The species that colonize and establish in these locales are determined by myriad factors— some stochastic, others intimately contingent upon the relationship between plot characteristics and species traits. We expect that the leading-edge populations of species observed in this study had a competitive advantage colonizing and establishing in the more burned and depauperate locales where the climate had shifted to become more similar to the colonizers' climatic niche than to the climatic niche of the historical populations. In other words, in areas where the climate had changed, species adapted to the new climate had a greater chance of establishing in fire-cleared spots. Further work will be necessary to provide a comprehensive understanding of the interactions between fire succession and climate-induced migration and their effect on post-fire community assembly.

The amount of climate change in the CMIP data across our study area is consistent with the observations and projections of other studies, particularly with regards to decreased summer precipitation and mean temperature increase^{42,43}. Precipitation and temperature variables are among the most important for determining plant distributions, and these variables can affect plant traits/distributions in concert and compound each other's effects. All but one species had a coupled response to both MSP and MTWM— six of eight species migrated towards higher MSP, of which all but one (*L. densiflorus*) also migrated towards lower MTWM. MSP and MTWM are both associated with drought-stress in trees, which can lead to mortality^{44–46}. Based on the

available information, the shift of six of the eight species in this study towards lower MTWM and higher MSP could reflect an increase in suitability for the migrating species or a decrease in suitability for the previous dominants, or some combination of the two. The available evidence does not address the relative roles of the two mechanisms.

The two species that did not migrate towards increased MSP or decreased MTWM were *P. contorta* and *A. lasiocarpa*, the only two species in this study that populate high-elevation subalpine regions. These trees are typically relegated to high altitude regions in the southern extent of the study area (Sierra Nevada for *P. contorta*, and the southern Rocky Mountains for both), and occupy lower elevation regions further north. Recent studies indicate that subalpine tree populations face decreased recruitment and range contraction due to climate change^{47,48}. Range expansions in northern low-elevation populations, coupled with range contraction or stagnation in high-elevation populations, could explain the unexpected shift of these two species towards increased MTWM and decreased MSP. Perhaps lower elevation populations shifted distributions to maintain climate equilibrium (towards decreased MTWM and increased MSP) but this trend was masked by the high altitude populations lack of shift or contraction.

The observed RS rates, when roughly converted from climatic distance to spatial distance, are also consistent with general expectations. Combining the observed average shifts in MTWM with the normal lapse rate of 6.5°C/km, we estimate that the non-subalpine trees shifted towards areas of lower MTWM by roughly +48m elevation in unburned plots, and +105m in burned. Subalpine tree (*P. contorta* & *A. lasiocarpa*) RS corresponds to -83 and -126m altitudinal shifts for unburned and burned plots, respectively. These values are within the range of RS in western Europe, where trees shifted up to 214m in mean elevation over the last century⁴⁹.

The sources of potential uncertainty in the interpretation of our results include (i) potential sink populations where seedlings occur but have not, and may not, reach maturity (ii) fire succession and fire-regime adaptations and (iii) the relationship between climatic distance and spatial distance (Equation 1).

An underlying assumption of the approach was that seedlings eventually mature into trees. This is, of course, not necessarily the case. We attempted to minimize the impact of sink populations on our results by excluding species where the direction of RS was not consistent among different life stages. We used diameter at breast height to delineate seedlings ($\text{dbh} < 2.5\text{cm}$), saplings ($2.5\text{cm} < \text{dbh} < 12.7\text{cm}$), trees ($\text{dbh} > 2.5\text{cm}$), and large trees ($\text{dbh} > 12.7\text{cm}$) and compared the RS vectors of seedlings and trees to saplings and large trees. We confirmed that all eight trees used in the primary analysis had consistent RS vector direction between these groups. However, while the sapling group likely contained fewer sink populations than the seedling group, it is still possible that some saplings were members of sink populations and would never reach reproductive maturity.

Fire adaptation and succession dynamics could confound the results where rates of RS into burned areas were partly due to post-fire colonization adaptations, creating two possible explanations for spread into burned areas. We minimized this effect by excluding species where the direction of RS in burned areas was inconsistent with the direction of RS in unburned areas—effectively removing species with traits that make post-fire colonization different from normal colonization. Only *Pinus albicaulis* was filtered out at this step, potentially because this tree occurred in the smallest number of burned plots ($N_{BS} + N_{BT} = 24$). Another caveat, more specifically pertaining to this analysis, is that the FIA recorded only fires that occurred within 5 years prior to the survey. Fires that burned 6 years prior could have affected the vegetation

regeneration/recruitment (and therefore RS rate) but would have been included in the NS and NT rather than the BS and BT groups. This could have resulted in an underestimation of the impact of fire on RS rate.

Further bias may have come from calculating climatic distance and assuming that it was an accurate proxy for spatial distance (Equation 1). The relationship is certainly not fixed, particularly across topographically diverse regions. A 400m horizontal distance will likely be much more climatically distant in a mountainous than a flatter region. Climatic distance is important in itself. Further, climatic and spatial distance are strongly correlated¹¹. One possible confounding effect would occur if burned plots are on steeper slopes. In this case, larger climatic distances in burned plots might not correspond to larger spatial distances. Slopes are significantly steeper in burned than in unburned plots ($p < .05$) (Appendix 2). The mean slope gradient across burned plots was 22.7°, while unburned plots averaged 18.6°. Steeper slopes may have inflated the RS rate in burned plots, but an average difference in slope of 4.1° explains only ~24% of the difference in mean elevation: 100 lateral meters on a 22.7° slope results in an endpoint 8.18m higher than on an 18.6° slope. Only the altitudinal shift of *P. contorta* and *Q. chrysolepis* (11% and 23% decrease in elevation in burned areas, respectively) could be entirely attributed to this, and the average percent increase in the elevation of other species in burned plots was 102%.

This study provides empirical evidence that wildfire increases the RS rate of tree species that are moving in response to recent climate change. Furthermore, we have argued that the increase in RS rate is likely a product of the reduction of the population size and density of the competitors due to wildfire. The findings of this study bolster previous work suggesting that competition is yet another barrier (in addition to dispersal limitations and geographic barriers)

that affects the ability of plant species to track their optimal climatic conditions as they move across landscapes.

Methods

Occurrence Data

Plot-level tree and seedling species lists were sourced from the USDA Forest Inventory and Analysis (FIA) program via the FIA DataMart tool (apps.fs.usda.gov/fia/datamart) in March of 2020 and analyzed using R version 4.0.0⁵⁰. The FIA data also include tree age, tree diameter at breast height (dbh), and the presence of fire disturbance at the plot (fires must have occurred, at most, 5 years prior to plot establishment and caused at least 25% tree mortality over at least 0.4 ha to have been recorded). FIA datasets are the most comprehensive continent-scale source for plot-level forest data in the U.S. In FIA Phase 2 data collection (sourced in this study), a plot is divided into four 168m² subplots and four 13.5m² microplots. Within subplots, all tree species (live or dead) with a dbh greater than 12.7cm are identified and tallied, and all seedlings are identified and tallied within microplots⁵¹.

We sourced all plots (33,838 total) within the Northwestern Forested Mountains and Marine West Coast Forest ecoregions of the continental U.S.⁵² (Fig. 1). All plots used in this study were surveyed between 2002 & 2017. For each species we separated the plots into unburned (N, control) and burned (B, treatment) groups. Within these two groups, novel seedling establishment was used as a proxy for RS as outlined in Zhu et al., 2012. Seedlings in plots with no adult tree (hereafter referred to as “tree”) of the species were considered the leading-edge of the migrating population. Subsequently, the FIA plots of each species were separated into 4 independent groups: (1) Plots that did not burn with only seedlings present (NS) (2) Plots that did

not burn with seedlings and trees present (NT) (3) Plots that burned with only seedlings present (BS) (4) Plots that burned with seedlings and trees present (BT). Species were removed from analysis if the number of plots was less than 5 in any of these four categories (NS, NT, BS, BT).

Because of the spatial uniformity of FIA sampling, spatial sampling bias is unlikely to be a major source of error in our analysis. However, seedlings were sampled in only a subset of each FIA plot, and it is possible that seedling species present in the full sampling plots were absent in the seedling microplots, potentially reducing the number of NS and BS plots.

Climate Data

Rasterized climate data (averaged from 1981-2010) were sourced at 30 arc-second resolution from the 2015 AdaptWest Project (<https://adaptwest.databasin.org>), constructed using ClimateNA v5.10 software⁵³. This climate data covers a period that ended seven years prior to the most recent FIA sampling, but we do not think this should have an appreciable effect on the results. We initially considered 8 possible climate variables, which were used for similar studies and recommended for climatic niche analysis because of their relevance to plant physiology: Mean Temperature of the Coldest Month, Mean Temperature of the Warmest Month, Mean Annual Precipitation, Ratio of Actual to Potential Evapotranspiration, Potential Evapotranspiration, Precipitation Seasonality, Mean Annual Temperature, and Growing Degree Days.^{54,55} We replaced Mean Precipitation Seasonality with its seasonal components, Mean Summer Precipitation and Mean Winter Precipitation, to make the results more interpretable and to isolate shifts in precipitation regimes across the study area, which varies (summer precipitation, particularly) across mountain, coastal, and mediterranean climates. We calculated the Variance Inflation Factor (VIF) for the set of 9 variables using the R package *usdm*⁵⁶ and incrementally excluded collinear variables until $VIF < 10$, as recommended⁵⁷, leaving the 3

climate variables with the least collinearity (see Appendix 3 for more information). The resulting climatic variables were: Mean Temperature of the Warmest Month (MTWM), Mean Summer Precipitation (MSP), Mean Winter Precipitation (MWP).

Species Selection

The climatic difference between seedling-only plots and tree-and-seedling plots may not represent the actual RS direction of a species. For example, seedling establishment may represent sink populations that occur in areas that will not support a reproducing population in the future. To ensure that we included only species for which we could confidently estimate the direction of RS, we compared the climatic RS vector of NS and NT plots with the RS vector of unburned sapling plots (NJ), with dbh between 2.5cm and 12.7cm, and unburned large tree (NG) plots, with dbh greater than 12.7cm⁹. We determined the consistency of the RS direction between the different life stages by calculating the component of the seedling RS vector, $\overrightarrow{RS}_{seed}$, that pointed in the same direction as the sapling RS vector, $\overrightarrow{RS}_{sapling}$, i.e. the dot product of the normalized RS vectors in climate space, $\frac{\overrightarrow{RS}_{seed} \cdot \overrightarrow{RS}_{sapling}}{|\overrightarrow{RS}_{seed}| |\overrightarrow{RS}_{sapling}|}$. Figure 5 provides a graphical explanation of this process. We used the cutoff of 50% vector agreement to exclude species where the RS direction was not consistent across life stages.

The direction of the RS vectors may differ significantly between the unburned and burned plots, possibly because of species-specific adaptations that affect colonization/regeneration after fire. To avoid the difficulty of comparing and interpreting RS rates of groups that are migrating in different directions, we also excluded species for which the cosine of the angle between RS vectors in burned and unburned plots was less than 0.5 (Figure 5).

Calculating Climatic Niche Difference and RS Rate

The RS rate was proxied by the climatic distance between source populations and leading-edge populations, i.e. the difference between the climatic niche of seedling-only plots and the plots with both trees and seedlings of a species (eq. 1).

$$r_i = \frac{DG_i}{t} \approx \frac{DC_i}{A_{Ti}-A_{Si}} \quad (1)$$

Where r_i is the RS rate and i is either burned (B) or unburned (N), DG is the geographic RS distance per time (t), DC is the climatic RS distance, per time unit defined by the mean age difference between mature trees (A_T) and seedlings (A_S). The Euclidean distance between the centroids for NS and NT and between BS and BT (derived from the magnitude of the climate RS vectors described above) give DC_N and DC_B , respectively. We do not have information on A_T and A_S , but we have no reason to expect them to be different between burned and unburned plots. Therefore, we use the ratio of DC_B to DC_N as our primary measure of whether RS distances are greater in burned plots.

Another metric for climatic niche difference, Schoener's D, was calculated using a modified R script⁵⁸ that calculates the two principal components which describe the most variation in climate space across NS and NT and across BS and BT, and then measures the difference between the kernel-smoothed component scores for the two pairs of plots. The statistical significance of Schoener's D is determined with the *niche equivalency test* of Broennimann et al 2012⁵⁸.

Lower values of Schoener's D and greater values of DC in burned plots support the hypothesis that fire facilitates RS.

Additional Analyses

To test the robustness of our results to different sets of climate parameters, we compared the results presented in this manuscript with a suite of results obtained from the use of different

sets of climate variables. We reanalyzed our data after adding each variable that was excluded in the multicollinearity analysis (Appendix 3), adding variables in the order of increasing VIF values for all variables beneath the threshold of $VIF = 10$: $\frac{Actual\ Evapotranspiration}{Potential\ Evapotranspiration}$, Mean Temperature of Coldest Month, then Potential Evapotranspiration. These 3 additional sets of results did not differ appreciably from our primary results— Schoener’s D and Euclidean centroid distance consistently indicated that RS rates were greater in plots that burned (Appendix 4).

To ensure that the threshold minimum sample size did not greatly impact the results, we repeated our analysis of RS rates for minimum sample size of presence in 5, 10, and 15 FIA plots. The threshold minimum sample size affects the number of species analyzed but not the conclusion that fire facilitates RS (Appendix 5). We focus on the analysis using a minimum sample size of 5, because the number of species meeting the threshold decreased sharply as the threshold increased. Furthermore, two species with $N_{BS} = 5$ passed the RS vector direction vetting, indicating that this sample size was sufficient to estimate an RS vector that was consistent with populations of larger sample sizes. We also verified that other decisions regarding species exclusion, such as species vetting due to RS vector agreement between life stages and burned-unburned plots, did not produce results that contradicted our conclusions (Appendix 6).

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Contributions

A.P.H. and C.B.F designed the thesis and research jointly, and A.P.H. conducted the data analysis and wrote the first draft of the manuscript. Both authors worked on subsequent revisions to both methodology and manuscript.

Competing Interests

The authors declare no competing interests.

Data Availability

The climate and plant occurrence data used to support the findings of this study are available from the AdaptWest Project (<https://adaptwest.databasin.org/>) and Forest Inventory Analysis (<http://apps.fs.usda.gov/fia/datamart>), respectively.

Code Availability

R scripts used in this study can be found at https://github.com/avephill/wildfire-plant_RS

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Tables

Species	# of Plots				Range Shift Vector Agreement	
	Inside Fire		Outside Fire		Between Life Stages	Inside vs. Outside Fire
	Trees & Seedlings	Novel Seedlings	Trees & Seedlings	Novel Seedlings	(NS-NT vs. NJ-NG)	(BS-BT vs. NS-NT)
<i>Abies grandis</i>	43	11	2543	523	81.647%	95.492%
<i>Abies lasiocarpa</i>	99	11	3301	514	53.182%	79.249%
<i>Lithocarpus densiflorus</i>	35	5	400	97	67.314%	66.866%
<i>Pinus contorta</i>	167	21	1866	209	61.769%	97.354%
<i>Pinus ponderosa</i>	58	18	1143	211	97.231%	93.45%
<i>Populus tremuloides</i>	11	56	336	267	60.676%	95.91%
<i>Pseudotsuga menziesii</i>	185	12	5785	563	84.591%	99.229%
<i>Quercus chrysolepis</i>	62	11	349	121	98.436%	75.337%

Table 1. Summary of the sample sizes and vector agreement values— values that were used to determine the species included in further analysis.

Species	Schoener's D		Centroid Distance	
	Inside Fire	Outside Fire	Inside Fire	Outside Fire
<i>Abies grandis</i>	0.551*	0.566*	0.129	0.185*
<i>Abies lasiocarpa</i>	0.637*	0.721*	0.455	0.221*
<i>Lithocarpus densiflorus</i>	0.512*	0.796*	1.269*	0.201*
<i>Pinus contorta</i>	0.555*	0.605*	0.263	0.226*
<i>Pinus ponderosa</i>	0.544*	0.633*	0.827*	0.447*
<i>Populus tremuloides</i>	0.537*	0.683*	0.273	0.178*
<i>Pseudotsuga menziesii</i>	0.428*	0.557*	0.902	0.419*
<i>Quercus chrysolepis</i>	0.644	0.815*	0.243	0.248*

Table 2. Summary of the climatic niche difference metrics. Schoener's D and Centroid distance were tested for statistical significance using the niche equivalency test and Hotelling's T^2 Test, respectively. Values appended with * indicate statistical significance ($p < .05$). Lower D and higher centroid distance values suggest greater niche difference.

577
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579

Figure 1

580

581 **Figure 1.** Plot of the study area. The Northwestern Forested Mountains and Marine West Coast Forest ecoregions
582 (thin black outline) of the northwestern continental United States determined the extent of the FIA plots (blue
583 points) that were sourced.

584

585 **Figure 2**

586

587 **Figure 2.** The scaled and centered PCA plot of the climatic niches of the leading-edge population (plots with only
588 seedlings) and source population (plots with both seedlings and trees) of *P. ponderosa*. PC1 and PC2 explain 84% of
589 the variation across all 3 climatic variables. Centroids are shown as large circles.

590

Figure 3

Figure 3a,3b. Box plots of the average difference between leading-edge populations and source populations (i.e. RS rate) for each climate variable. White dots indicate the mean while white bars indicate the median. **3a** keeps the directionality of RS and shows the relative difference of RS rates across each variable. By contrast, **3b** shows the value of RS rate, relative to unburned plots.

599 **Figure 4**

600

601 **Figure 4.** Boxplot showing the scaled difference between average 1981-2010 climate and average 1961-1990
602 climate across the study area (i.e. $\overline{Climate_{1981-2010}} - \overline{Climate_{1961-1990}}$). Observed climatic shifts were statistically
603 significant according to a two-sided t-test, with $p < .05$ for each climate variable. The MTWM increased at a
604 greater magnitude than the precipitation variables decreased. Climatic shifts specific to the distribution of each
605 species can be found in Appendix 1.

606

607 **Figure 5**

608

609 **Figure 5.** A synthesized example of the RS vector-direction comparison methodology. After scaling the
610 environmental variables across the study area, we plotted the RS vectors (exemplified here by $\vec{A}$ and $\vec{B}$) with the
611 initial point of each vector at the centroid of the source population and the terminal point of each vector at the
612 centroid of the leading-edge population (a). We then translocated the vectors to the origin and found the angle θ
613 between them (b) and calculated the cosine of θ which is equivalent to $\frac{|\vec{A}_{\parallel}|}{|\vec{A}|}$, i.e. the component of the normalized $\vec{A}$
614 that lies along normalized $\vec{B}$ (c).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [HillField2020Supplement.pdf](#)