

Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes

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Abstract. Altered fire regimes can drive major and enduring compositional shifts or losses of forest ecosystems. In western North America, ponderosa pine and dry mixed-conifer forest types appear increasingly vulnerable to uncharacteristically extensive, high-severity wildfire. However, unburned or only lightly impacted forest stands that persist within burn mosaics—termed fire refugia—may serve as tree seed sources and promote landscape recovery. We sampled tree regeneration along gradients of fire refugia proximity and density at 686 sites within the perimeters of 12 large wildfires that occurred between 2000 and 2005 in the interior western United States. We used generalized linear mixed-effects models to elucidate statistical relationships between tree regeneration and refugia pattern, including a new metric that incorporates patch proximity and proportional abundance. These relationships were then used to develop a spatially explicit landscape simulation model. We found that regeneration by ponderosa pine and obligate-seeding mixed-conifer tree species assemblages was strongly and positively predicted by refugia proximity and density. Simulation models revealed that for any given proportion of the landscape occupied by refugia, small patches produced greater landscape recovery than large patches. These results highlight the disproportionate importance of small, isolated islands of surviving trees, which may not be detectable with coarse-scale satellite imagery. Findings also illustrate the interplay between patch-scale resistance and landscape-scale resilience: Disturbance-resistant settings (fire refugia) can entrain resilience (forest regeneration) across the burn matrix. Implications and applications for land managers and conservation practitioners include strategies for the promotion and maintenance of fire refugia as components of resilient forest landscapes.

Key words: burn severity; dispersal; fire refuge; landscape memory; landscape simulation models; refugia; scale; spatial resilience.

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INTRODUCTION

Changing fire regimes, associated with climate and land use, have the potential to catalyze large-scale transformations of forest ecosystems

(Savage and Mast 2005, Serra-Diaz et al. 2018). Wildfire has propelled a remarkable range of adaptations by Earth's flora (Pausas and Keeley 2009), with specific traits adaptive for some, but not all, fire regimes (Keeley et al. 2011). For

example, stand-replacing fire regimes have selected for an interrelated suite of traits within the genus *Pinus* that promote flammability and post-fire seedling establishment (e.g., serotinous cones), whereas low-severity fire regimes are linked to fire-resistant traits such as self-pruning and thick bark (Schwilk and Ackerly 2003). As such, changes in fire regimes can leave formerly well-adapted species highly vulnerable. For example, escalating fire frequency may preclude the interval required for woody plant maturation and reproduction (Enright et al. 2015). Conversely, shifts from frequent low-severity surface fires toward stand-replacing canopy fire can tip frequent fire-adapted forests, woodlands, and savannas toward alternate states (Adams 2013). In western North America, ponderosa pine (*Pinus ponderosa*) and dry mixed-conifer forest types were highly resistant to low-severity fires with short return intervals prior to European settlement, but this fire regime was impeded over a century ago (Covington and Moore 1994, Allen et al. 2002). Resultant fuel accumulations, interacting with climate drivers, have led to fires with uncharacteristically large high-severity patches in these systems (Fornwalt et al. 2016), which can initiate shifts toward non-forested states (Savage and Mast 2005, Airey Lauvaux et al. 2016, Chambers et al. 2016, Coop et al. 2016, Barton and Poulos 2018, Haffey et al. 2018).

Given the vulnerability of forest landscapes to changing fire regimes and other anthropogenic pressures, there is an impelling need to understand and promote their ecological resilience (Millar et al. 2007, Reyer et al. 2015). Resilience is the capacity of a system to return to a reference state following temporary changes imparted by a disturbance (Grimm and Wissel 1997). The term “recovery” (following Falk 2017) may also represent such a return toward a pre-disturbance state—for example, the re-establishment of trees following high-severity fire in a formerly forested landscape. In contrast, resistance implies a system that remains relatively unchanged through disturbance. In frequent-fire forest types, many authors agree that fuel reduction and restored fire regimes can enhance disturbance resistance and recovery potential following disturbance (Millar et al. 2007, Moritz et al. 2011, Falk 2017, Walker et al. 2018). Spatial heterogeneity is also considered a key element of resilience in these

systems: Fine-grained mosaics of openings and forest patches of varying age classes and species composition may impede disturbance spread and promote compositional and structural diversity (Churchill et al. 2013, Hessburg et al. 2015). However, an understanding of the contribution of landscape spatial characteristics to resilience processes—referred to as spatial resilience (Cumming 2011, Allen et al. 2016)—remains a relatively undeveloped research theme.

Wildfires produce considerable landscape heterogeneity that includes unburned or lightly burned patches, termed fire refugia (Camp et al. 1997, Krawchuk et al. 2016). Meddens et al. (2018) further define fire refugia as “landscape elements that remain unburned or minimally affected by fire, thereby supporting post-fire ecosystem function, biodiversity, and resilience to disturbances.” The duration and location of fire refugia depend on landscape factors and fire behavior. Persistent fire refugia that endure through many fire cycles are generally linked to topographic features that limit fire spread and may be associated with different vegetation types (Wood et al. 2011, Adie et al. 2017) or old-growth forest structure (Rogeanu et al. 2018). However, refugium occurrence within a burn can also be shaped by less predictable and dynamic factors such as stand history, or stochastic processes such as wind shifts during burning. Such refugia are more likely to be transient in nature and may burn severely in subsequent fire (Kolden et al. 2017). Fire refugia may be distinguished from the rest of the burn matrix as areas exhibiting little change in satellite-based reflectance metrics (e.g., Landsat-derived differenced Normalized Burn Ratio [dNBR]), though such areas are likely to include a wide range of vegetation types and non-vegetated areas (Meigs and Krawchuk 2018). For applications specific to forests, refugia may be delineated as locations that retain live tree canopy following fire, which may include small and isolated patches not detectable using 30-m resolution Landsat imagery.

As disturbance-resistant locations that can sustain species and serve as source populations for recolonization, refugia hold substantial promise as components of resilient landscapes (Hannah et al. 2014). Fire refugia that retain mature trees through disturbance may serve importantly as seed sources for post-fire landscape reforestation

(Landesmann and Morales 2018, Downing et al. 2019), thus serving as elements of spatial resilience. Within contemporary high-severity burn interiors in ponderosa pine and dry mixed-conifer forests western North America, numerous prior studies have demonstrated that regeneration by obligate-seeding tree species is limited by distance from surviving seed sources (Bonnet et al. 2005, Haire and McGarigal 2010, Chambers et al. 2016, Kemp et al. 2016, Owen et al. 2017, Haffey et al. 2018). However, much of this work has related regeneration densities to simple Euclidean measures of distance to burn perimeters (i.e., seed walls) or the edges of large patches of trees. It is not known how well relationships between seed-source distance and forest recovery may be extended across a wide range of forest patch sizes and small, island-like refugia. Further, any given location within a burn may receive propagules from multiple sources, and as such, a single measure of distance may not adequately represent recovery potential. Forest composition may include species with different regeneration strategies, and thus, spatial associations between fire refugia and regeneration are also likely to vary across species.

Because fire refugia can occur as relatively discrete forested patches within severely burned landscapes, assessing their capacity to shape post-fire recovery and influence spatial resilience lends itself to spatially explicit landscape simulation modeling approaches. Landscape simulation models are well-suited to explore post-fire landscape dynamics (He and Mladenoff 1999), and they have increasingly been used to assess the effectiveness of interventions to retain forests under varying disturbance scenarios (Halofsky et al. 2014, Barros et al. 2018). Efforts have also applied landscape simulation models toward the characterization of ecological resilience (Peterson 2002, Keane et al. 2018).

The impetus of our study was to assess how fire refugia influence landscape resilience across ranges of patch sizes and abundances, and tree species mixtures, with a focus on forests of the interior western United States considered vulnerable to severe fire. Specifically, our study objectives were to (1) characterize tree species composition and seedling abundances within forested refugia and in areas that burned at high severity, and (2) evaluate statistical relationships

between tree regeneration and new, composite metrics of refugia proximity and abundance. Finally, with the relationships established above, we developed a spatially explicit simulation model to (3) investigate how refugia patch size and landscape proportion affect the rate and extent of forest recovery for different species assemblages. We asked how patterns of tree regeneration differed in post-fire landscapes composed of many, small vs. few, large refugia. Conceptually, we explored how the quantity and apportionment of disturbance-resistant elements within a landscape matrix might shape the resilience of that matrix.

MATERIALS AND METHODS

Study area

Data were collected during the summer of 2017 within the perimeters of 12 wildfires that occurred between 2000 and 2005 (Fig. 1), resulting in a snapshot of forest recovery 12–17 yr post-fire. Criteria for study site selection included (1) prior to fire, burns were occupied primarily by ponderosa pine and/or dry mixed-conifer forest types (based on available vegetation maps, communications with land managers, and/or experience of the authors), (2) burns included a substantial stand-replacing component, and (3) burns occurred over a comparable time frame (12–17 yr before sampling) to have allow for examination of patterns of natural regeneration.

Such that findings could be generalized across ponderosa pine and dry mixed-conifer forest types in the western United States, sampled burns occurred across a broad range of environmental conditions (Table 1). Study sites occurred in three different ecoregions (Omernik and Griffith 2014): the Blue Mountains (Oregon), the Southern Rockies (Colorado and northern New Mexico), and Arizona/New Mexico Mountains (central and northern Arizona). The Blue Mountains are composed of several small mountain ranges dissected by steep river canyons in northeastern Oregon, collectively comprising a south-to-north precipitation gradient. The climate of study burns in this ecoregion (747 Complex, Burnt Cabin, Hash Rock, and Roberts Creek) is generally cool, with mean annual temperature (MAT) ranging from 4.4°C to 7.3°C, but mean

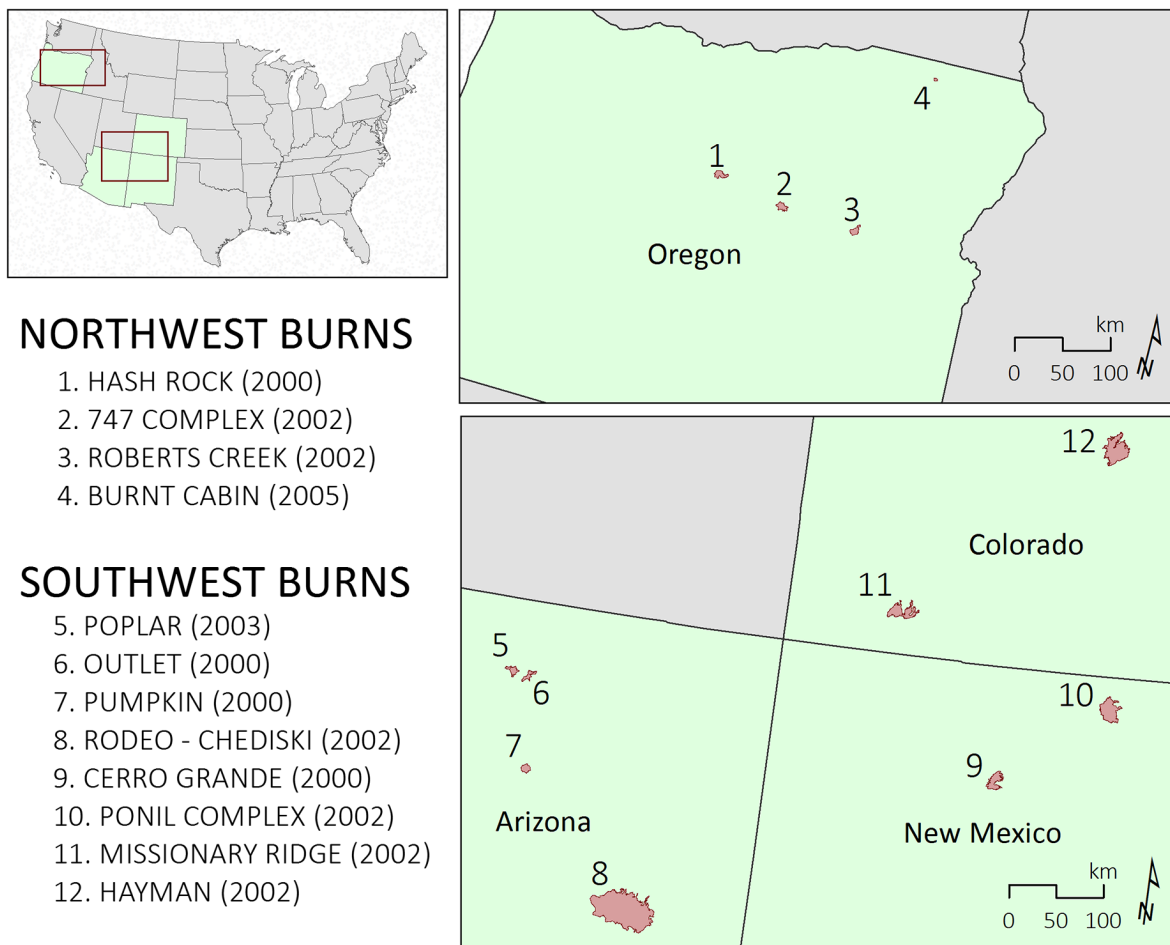


Fig. 1. Locations of sampled burns in the western United States.

annual precipitation (MAP) varying substantially, between 466 and 1198 mm (Table 1; climate data from Hijmans et al. 2005). A broader description of these sites is available in Downing et al. (2019). The Southern Rockies comprise numerous, large mountain ranges in Colorado and northern New Mexico encompassing steep elevational and climatic gradients. Three of these burns (Cerro Grande, Missionary Ridge, and Ponil Complex) occupy a mix of relatively flat terrain on moderate elevation mesas and steep-sided canyons; the Hayman burn landscape is more rolling with steep hills. Southern Rockies sites are generally warmer and drier than those farther north, with MAT ranging from 5.2°C to 8.9°C and MAP from 492 to 734 mm (Table 1). Finally, we sampled four burns occurring across

a range of landforms in the Arizona/New Mexico Mountains ecoregion. The Poplar and Outlet burns occupy mostly flat landscapes on the Kaibab Plateau north of the Grand Canyon. The Rodeo–Chediski burn straddles the plateaus and canyons of Mogollon Rim; the Pumpkin burn is on an isolated volcanic mountain. Generally, these sites occupies the warmest and driest conditions, with MAT between 6.6°C and 10.6°C and MAP between 551 and 601 cm (Table 1).

Refugia mapping and neighborhood characterization

For each burn, we developed high-resolution maps of tree cover from which we stratified field sampling locations and generated spatial predictor variables for statistical models. Maps of live

Table 1. Attributes of study burns.

Burns	Year	Area (ha)	Proportion moderate + high severity	Study area, Ecoregion	MAT (°C)	MAP (mm)
747 Complex	2002	6475	0.22	NW, Blue Mountains	7.3	466
Burnt Cabin	2005	871	0.17	NW, Blue Mountains	6.2	1198
Cerro Grande	2000	17,919	0.51	SW, Southern Rockies	8.9	537
Hash Rock	2000	6945	0.41	NW, Blue Mountains	6.6	531
Hayman	2002	52,353	0.65	SW, Southern Rockies	6.7	503
Missionary Ridge	2002	27,891	0.53	SW, Southern Rockies	5.2	734
Outlet	2000	5801	0.44	SW, Arizona/New Mexico Mountains	8.0	589
Ponil Complex	2002	36,051	0.51	SW, Southern Rockies	7.8	492
Poplar	2003	6845	0.30	SW, Arizona/New Mexico Mountains	7.5	597
Pumpkin	2000	6510	0.38	SW, Arizona/New Mexico Mountains	6.6	610
Roberts Creek	2002	5689	0.55	NW, Blue Mountains	4.4	857
Rodeo–Chediski	2002	186,873	0.68	SW, Arizona/New Mexico Mountains	10.6	551

Notes: Burn area and proportion of moderate + high severity from the Monitoring Trends in Burn Severity (Eidenshink et al. 2007); level III ecoregion based on Omernik and Griffith (2014); 30-yr (1981–2020) mean annual temperature (MAT) and precipitation (MAP) from WorldClim (Hijmans et al. 2005).

tree cover following wildfire—operationally defined as forested fire refugia for the purposes of this research—were produced from post-fire, 1-m resolution National Agriculture Imagery Program (NAIP) imagery. We developed a semi-automated, object-based classification as follows. First, we accessed fire perimeter polygons from the Monitoring Trends in Burn Severity project (Eidenshink et al. 2007) and NAIP imagery captured ca. 5 yr post-fire to ensure second-order fire effects had occurred. Images were segmented into objects with similar spectral and spatial properties. Objects representing live, post-fire tree canopy and non-forested areas were selected as training samples ($n > 100$ for each class) using onscreen selection in a supervised maximum-likelihood classification of each segmented image. We applied a 7×7 majority filter to reduce isolated pixels and converted forest pixels into polygons, closing any holes $< 50 \text{ m}^2$ (Chambers et al. 2016). Following visual assessment of the object-based classification, some additional manual editing was employed to exclude polygons misclassified as forest and include those misclassified as non-forest. Edited polygons were converted back to a 1-m resolution binary raster format for imagery- and field-based accuracy assessments. We refer to these two classes as (1) forested refugia and (2) non-forest in the text below. Imagery-based accuracy assessments utilized 100 randomly stratified validation points in each class; total accuracy ranged from 91% to

95%; field-based ground truth data yielded total accuracy percentages ranging from 90% to 97%.

We used the maps described above to characterize the spatial location of all pixels relative to refugia. This information was then used to stratify field samples to ensure representation across broad gradients of refugium proximity and density, and to generate spatial predictor variables for use in subsequent analyses of tree regeneration. For each pixel, we calculated four spatial predictor variables. (1) Euclidean distance (D) was measured to the nearest refugium (meters; within refugia all distances were 0). (2) Euclidean distance squared (D^2) was calculated because propagules disperse across two dimensions, which should produce a geometrical decrease away from seed sources. However, neither of these metrics accounts for variation in seed quantity due to differences in seed-source patch size nor for seed rain from more than one seed source: At any given Euclidean distance, greater propagule availability would be expected for pixels proximal to a large vs. a small seed source, and multiple vs. a single patch. Accordingly, we calculated two metrics incorporating both refugium proximity and density as follows. (3) Distance-weighted density (DWD) is defined as

$$\text{DWD} = \sum_{i=1}^N \frac{1}{(d_i + 1)}$$

where i represents forested refugium pixels and d is distance from the focal cell. (4) Distance-

squared weighted density (D^2WD) was calculated similarly, though with a squared distance term, as

$$D^2WD = \sum_{i=1}^N \frac{1}{(d_i^2 + 1)}.$$

To reduce computational time, DWD and D^2WD were calculated from maps that were rescaled to a cell size of 10 × 10-m cells employing a majority rule, though this likely reduced our ability to discern influences of very small patches. To explore the potential influence of refugium density across a range of scales, we calculated DWD and D^2WD from a moving window over a range of sizes including a radius of 10, 50, 100, 150, and 300 m. Analyses were conducted in R (R Core Team 2016) using the package raster (Hijmans et al. 2017).

Field sampling

Within each burn, samples were stratified based on the forested refugia vs. non-forest map along a gradient of distance-weighted refugium density (metric 3 above, 150-m cell radius DWD). The DWD values were binned into four quartiles each for refugium and non-forest pixels. An equal number of points was generated randomly within each class. Plots were selected for sampling in the field such that at each burn, approximately one quarter of all sampling would occur within forested refugia and three quarters in non-forested areas. Areas within 150 m of the burn perimeter were excluded from sampling, and sampled points were required to have a separation of at least 150 m. To ensure sampling occurred in locations that were forested pre-fire (excluding, e.g., meadows and barren rock), within our non-forest class we excluded areas with dNBR < 400. Areas known to have reburned or that were subject to post-fire reforestation or salvage logging were also excluded. Finally, to facilitate efficient access, points were located >150 m but <1 km from roads and trails. Generally, 50 plots were sampled within each burn; 100 were sampled in the two largest burns: Hayman and Rodeo-Chediski.

Sample units consisted of a 5.64-m radius circular plot (100-m²) centered on each selected point. Spatial coordinates (UTM NAD 83) of each plot center were recorded, and photographs

were taken along the N-S axis of each plot. Individuals of all tree species were assigned to one of three categories: (1) residual (establishment predated the wildfire), (2) regeneration (establishment occurred after the fire), or (3) unknown. This categorization was facilitated by the large and distinct gap in age/size structure left by study fires. For all trees (defined as ≥1.37 m in height), we recorded species identity and diameter at breast height (DBH). For seedlings (<1.37 m), we tallied all individuals by species.

Statistical analysis

We utilized generalized linear mixed-effects models to assess relationships between tree seedling abundances and two classes of predictor variables related to refugium distance and density. In each case, our null hypothesis was that tree regeneration was not related to refugium density or proximity. Models were created and selected to predict seedling recruitment, μ_{seed} , in non-forest pixels outside of refugia within our 100-m² field-sampled plots. We developed models for regeneration for four tree species assemblages: (1) ponderosa pine, (2) obligate-seeding mixed conifer (primarily Douglas-fir and two true firs, *Abies concolor* and *Abies grandis*, but including all other obligate-seeding tree species other than ponderosa and lodgepole pine), (3) resprouting and serotinous species considered to be well-adapted to stand-replacing fire (aspen [*Populus tremuloides*], alligator juniper [*Juniperus deppeana*], and lodgepole pine), and (4) all tree species. Assemblage 1 represents a single species, ponderosa pine. The other mixed-species assemblages were modeled in part because relatively small sample sizes for species other than ponderosa pine precluded a robust analysis for each individual species. We recognize these groupings include variation in life-history traits but they are intended to be broadly representative of general patterns of post-fire regeneration across dry forest types. Assemblages 2 and 3 represent two groups of tree species with markedly divergent post-fire regeneration strategies (dependence on live tree seed sources for the former, not for the latter). Assemblage 4 generalizes the total capacity for post-fire tree regeneration by all species present within sampled landscapes.

For each assemblage, two groups of models were constructed; the first predicted measured

seedling counts and the second predicted annual, time-since-fire relativized counts (seedling tallies divided by the number of years since fire). The latter accounted for variation across burns in time-since-fire and also provided the foundation for annual time steps in the simulation models described below.

The structure of our seedling abundance data fits a negative binomial distribution in which variance increased quadratically with the mean (the `nbinom2` family in `glmmTMB`; Brooks et al. 2017). Variance of μ_{seed} , σ^2 , was defined as $\mu + (1/\theta)\mu^2$, where θ is a dispersion constant. To determine the strongest predictors of post-fire tree regeneration, we constructed four combinations of models for each response variable, each model including one simple distance term (D or D^2) and one weighted density metric (DWD or $D^2\text{WD}$). To examine the influence of refugium spatial pattern over a range of spatial scales, we assessed the influences of the weighted density metric at each window radius described previously (10, 50, ..., 300 m). Other combinations of predictor variables were not considered given collinearity and reduced interpretability. Burn identity (e.g., Table 1: 747, Burnt Cabin, Cerro Grande, ...) was included as a random effect to the intercept to account for geographic variation in climate, substrate, and other factors. For each assemblage modeled, we selected the strongest model based on lowest Akaike's information criterion score. All models were developed using the package `glmmTMB` (Brooks et al. 2017). The lognormal approximation of R^2 (or R^2_{GLMM} ; Nakagawa and Schielzeth 2013) was calculated for both the fixed effects (marginal R^2) and full model including random effects (conditional R^2) for each model as implemented in the `MuMIn` package (Barton 2019).

Simulation modeling

To explore how refugium patch size and abundance shape the rate and extent of forest recovery, we developed a series of spatially explicit simulation models parameterized with the statistical relationships developed above (Fig. 2). While many other environmental covariates (e.g., topography, climate, competition) are important determinants of post-fire tree regeneration, our intent was to focus

exclusively on the influence of refugium patch size and abundance. For each tree species assemblage, we incorporated the formula of the best fitting statistical model predicting time-relativized, mean annual recruitment into simulations of post-wildfire regeneration on fabricated landscapes. Models simulated regeneration at 1-yr time steps for 20 yr on a 1000×1000 pixel raster (a 10-km^2 landscape with 100-m^2 pixels). We limited simulation runs to 20 yr so as not to extrapolate substantially beyond our dataset interval or into time frames in which recruitment would be expected to decline and/or recruits could potentially bear seed. Patches representing refugia were generated using the `makeclass` function of package `landscapeR` (Masante 2017). Initial landscapes had a predefined number of equally sized refugia generated at random locations; patch size ranged from 1 to 100,000 pixels (0.01–1000 ha). Patch number ranged from 0 to 900,000 (depending on patch size: As patch size increased, fewer patches could be generated before filling the landscape). We simulated 85 distinct configurations of varying refugium area and number (provided in Appendix S1: Table S1). The remainder of the landscape represented areas burned at high severity; we refer to these pixels non-forest. For these, we calculated D and $D^2\text{WD}$. These values were held constant; the model assumed that tree seedlings did not contribute to seed rain until they were >20 yr old.

For each simulation year, annual recruitment (number of successful trials) within each non-forest pixel was based on drawing from the negative binomial (NB) distribution:

$$X \sim \text{NB}\left(\bar{x}, \bar{x} + \frac{1}{\theta}\bar{x}^2\right)$$

in which $\bar{x}$ represents the estimated μ_{seed} generated from the formula

$$\bar{x} = e^{\beta_0 + \beta_1 D_i + \beta_2 D^2\text{WD}_i}$$

β_0 , β_1 , and β_2 represent the regression coefficients calculated previously (note that for some seedling assemblages, β_1 and/or β_2 may have a value of 0); D_i represents the distance to the nearest forested pixel assigned to non-forested pixel i ; and $D^2\text{WD}_i$ represents the $D^2\text{WD}$ score assigned to non-forested pixel i . The dispersion coefficient $\hat{\theta}$ was parameterized from the negative binomial

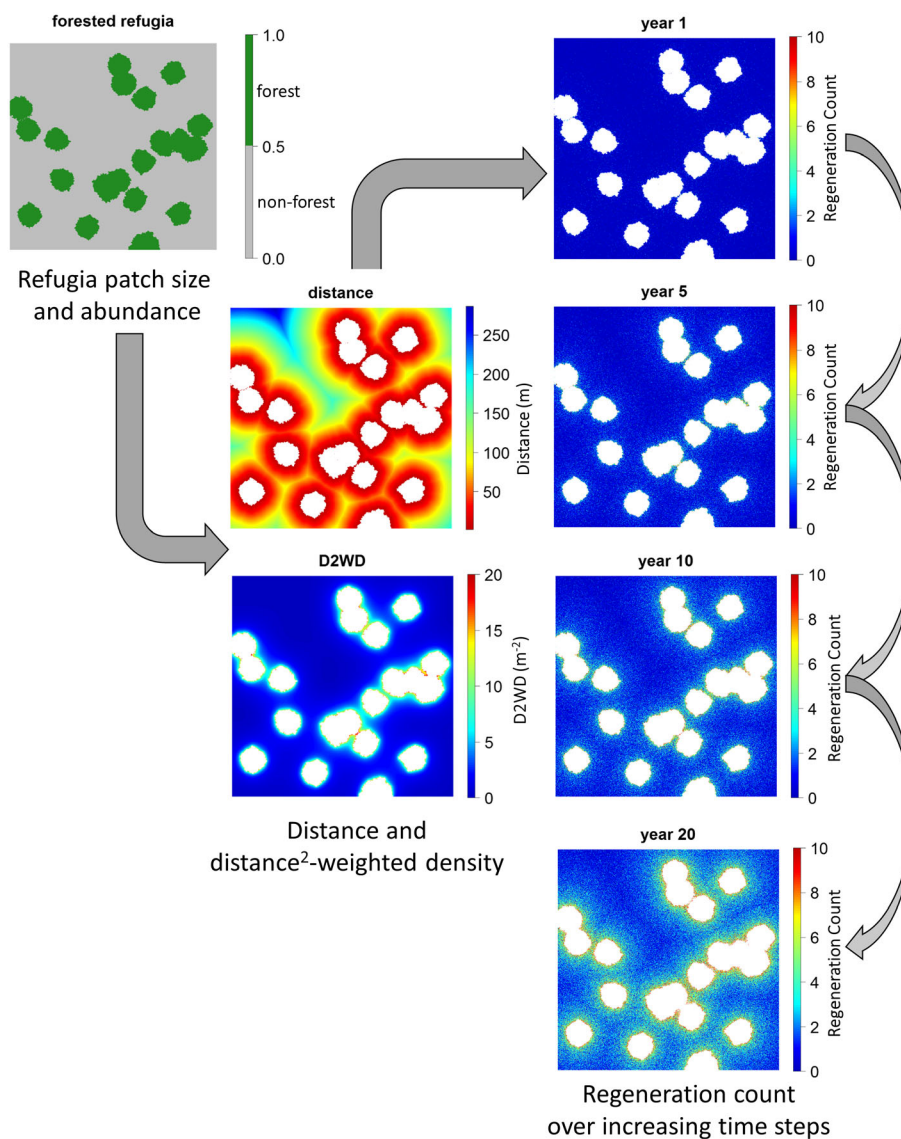


Fig. 2. Schematic of spatially explicit simulation model of tree regeneration in burn interiors as a function of the size and abundance of forested refugia. Simulation surfaces represent a 10×10 -km landscape with 10^6 cells each 10×10 m.

statistical models described previously. A single value was drawn from this distribution for each non-forested pixel per iteration. Values were summed across time steps (a non-forested pixel could recruit seedlings throughout the 20-yr simulation period).

We conducted 340 simulations, each over 20 annual time steps. For each simulation, at years 1, 5, 10, and 20, we counted the total number of

non-forested pixels, the number of non-forested pixels with $0, \geq 1, \geq 5$, and ≥ 10 recruits (equivalent to recruitment densities of 100, 500, and 1000 ha^{-1}), and the maximum number of recruited seedlings. Regeneration densities of $\geq 1, \geq 5$, and ≥ 10 individuals/pixel (100, 500, and 1000 ha^{-1}) were selected as thresholds for forest recovery to visualize relationships between refugia pattern and forest recovery.

RESULTS

Attributes of refugia, residual trees, and regeneration

Within our 12 study burns, we sampled 182 plots within refugia and 504 plots in non-forest areas burned at high severity. Within refugia, 167 plots (92%) showed clear evidence of recent surface fire such as bole scorch and char; only 15 sample plots (8%) did not display evidence of recent burning. Refugia were generally characterized by low but variable stand density, averaging 314 ± 342 trees/ha (Appendix S1: Table S2; values represent mean ± 1 standard deviation (SD); high SDs relative to the mean indicate high variability). Refugia displayed low, but variable, basal area, averaging 93.1 ± 93.6 m²/ha (Table 2).

Dominance was generally by one or a few large trees within each 100-m² sample plot—mean tree DBH was 25.2 ± 17.4 cm. Ponderosa pine accounted for nearly half of all residual trees, greater than half of total basal area (Table 2) and occurred in 58% of all sample plots. Three other species frequently occurred within refugia, often as co-dominants: Douglas-fir (occurring in 25% of sampled refugia), grand fir (*A. grandis*) in the northwestern burns (12%), and white fir (*A. concolor*) in many southwestern sites (8%). Trees of 11 other species were recorded infrequently in sampled refugia, varying across the geography of the study fires (Table 1). At 22/182 refugium sites (12%), no live residual trees occurred within sample units, though these plots fell within forested refugia, reflecting

Table 2. Frequency (proportion of plots occupied), density, and basal area (± 1 SD) of post-fire residual trees; frequency and density of tree regeneration in and out of forested refugia, by species.

Common name	Scientific name	Within refugia (<i>n</i> = 182)					Out of refugia (<i>n</i> = 504)		Study area
		Frequency	Residual		Regeneration		Regeneration		
			Basal area (m ² /ha)	Density (ha ⁻¹)	Frequency	Density (ha ⁻¹)	Frequency	Density (ha ⁻¹)	
White fir	<i>Abies concolor</i>	0.08	6.5 ± 27.6	17 ± 65	0.11	133 ± 655	0.08	37 ± 204	SW
Grand fir	<i>Abies grandis</i>	0.12	15.3 ± 63.0	60 ± 259	0.17	1424 ± 7409	0.14	455 ± 2366	NW
Subalpine fir	<i>Abies lasiocarpa</i>	0.00	0	0	0.01	5 ± 60	0.01	2 ± 19	NW, SW
Alligator juniper	<i>Juniperus deppeana</i>	0.01	0.0 ± 0.4	2 ± 23	0.02	5 ± 35	0.03	7 ± 51	SW
Oneseed juniper	<i>Juniperus monosperma</i>	0.01	0.0 ± 0.3	1 ± 7	0.01	2 ± 22	0.02	2 ± 19	SW
Western juniper	<i>Juniperus occidentalis</i>	0.01	0.2 ± 2.1	2 ± 17	0.04	21 ± 176	0.02	9 ± 82	NW
Utah juniper	<i>Juniperus osteosperma</i>	0.01	0.1 ± 1.0	3 ± 37	0.00	0	0.00	1 ± 16	SW
Rocky Mountain juniper	<i>Juniperus scopulorum</i>	0.01	0.5 ± 4.7	1 ± 10	0.01	1 ± 7	0.01	1 ± 12	SW
Western larch	<i>Larix occidentalis</i>	0.01	0.2 ± 2.8	1 ± 7	0.06	74 ± 397	0.08	217 ± 1455	NW
Engelmann spruce	<i>Picea engelmannii</i>	0.03	2.1 ± 21.8	15 ± 113	0.05	28 ± 211	0.04	104 ± 1035	NW, SW
Colorado blue spruce	<i>Picea pungens</i>	0.01	1.5 ± 18.1	4 ± 43	0.02	4 ± 33	0.01	1 ± 19	SW
Lodgepole pine	<i>Pinus contorta</i>	0.02	0.8 ± 0.8	10 ± 95	0.05	33 ± 178	0.08	350 ± 2622	NW, SW
Two-needle pinyon	<i>Pinus edulis</i>	0.03	0.6 ± 4.1	7 ± 49	0.03	6 ± 45	0.00	0 ± 4	SW
Ponderosa pine	<i>Pinus ponderosa</i>	0.58	49.5 ± 70.3	137 ± 187	0.47	509 ± 1292	0.56	683 ± 2374	NW, SW
Quaking aspen	<i>Populus tremuloides</i>	0.02	0.5 ± 4.9	2 ± 18	0.14	471 ± 171	0.21	977 ± 3182	SW
Douglas-fir	<i>Pseudotsuga menziesii</i>	0.25	15.4 ± 43.6	52 ± 153	0.29	315 ± 1114	0.24	219 ± 901	NW, SW
All species		0.88	93.1 ± 93.6	314 ± 342	0.72	3031 ± 8652	0.77	3066 ± 6899	

Notes: Because our data are not normally distributed standard deviations (SD) frequently exceed the mean. We also indicate in which portion of the study area (NW, northwest; SW, southwest) species occurred.

a wider spacing of tree boles than our relatively small, 5.64-m radius plots.

Within refugia, recent tree regeneration was composed largely of ponderosa pine, with 47% of forested plots containing at least one ponderosa pine seedling, and an average of 509 ± 1292 seedlings/ha (mean $\pm$ 1 SD; Table 2). However, regenerating Douglas-fir (in 29% of sampled refugia), true firs (collectively occurring in 28%), and aspen (14%) were also abundant. Together, regeneration by one or more tree species occurred in 73% of refugia and averaged 3031 ± 8652 stems/ha.

Outside refugia, ponderosa pine seedlings occurred in 56% of plots with a mean density of 683 ± 2374 stems/ha (Table 2). Ponderosa pine seedling densities declined with increasing

distance from refugia and decreasing D^2WD (Figs. 3a, 4a, 5). Seedlings of true fir species and Douglas-fir occurred in 22% and 24% of samples (Table 2). These were generally found at the highest densities within refugia and declined rapidly with increasing distance and decreasing D^2WD (Figs. 3b, 4b). Two species showed increased regeneration away from refugia relative to their frequencies and densities as residual trees: lodgepole pine (at 8% of non-forested sites, predominantly in the northwestern burns) and aspen (at 21% of non-forested sites, restricted to southwestern burns; Table 2). Regeneration by these resprouting and serotinous species increased away from refugia and where refugium density was low (Figs. 3c, 4c). Abundance of regeneration by all tree species in severely

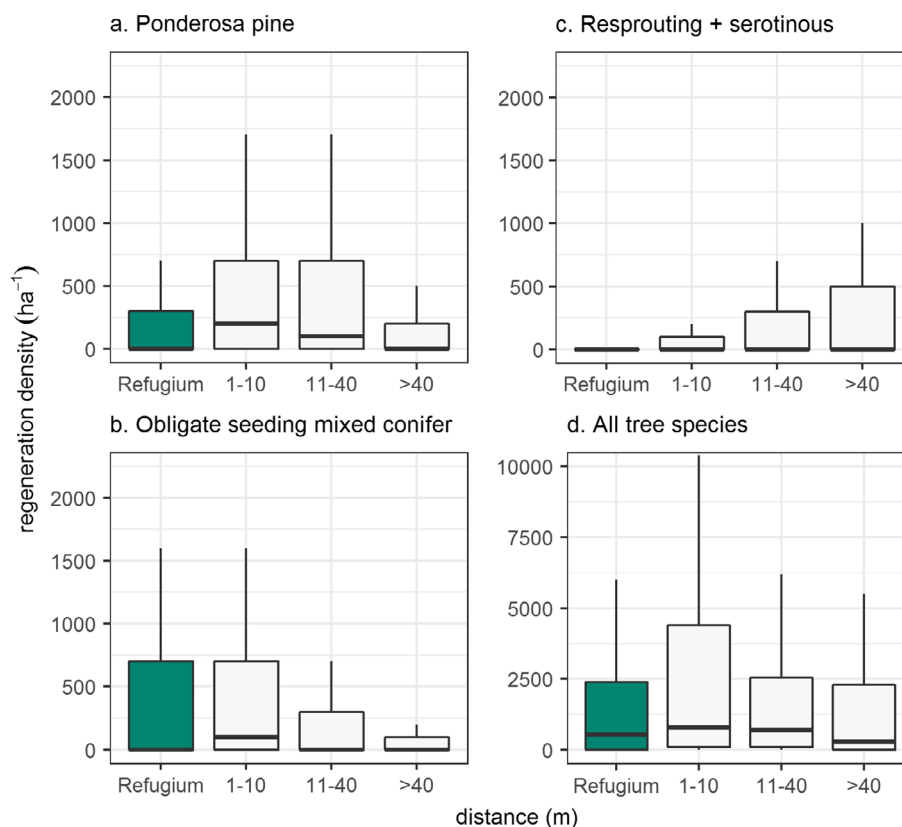


Fig. 3. Densities of regenerating stems within refugia (green, leftmost bar in each graph) and in burn interiors outside of refugia (gray bars) as a function of increasing minimum distance from tree seed sources. Distance (m) is from sample site to the nearest forested fire refugia. Tree regeneration groupings are as follows: (a) ponderosa pine; (b) obligate-seeding mixed-conifer species (all species excluding ponderosa pine, aspen, lodgepole pine, and alligator juniper); (c) resprouting and serotinous species including aspen, lodgepole pine, and alligator juniper); and (d) all tree species.

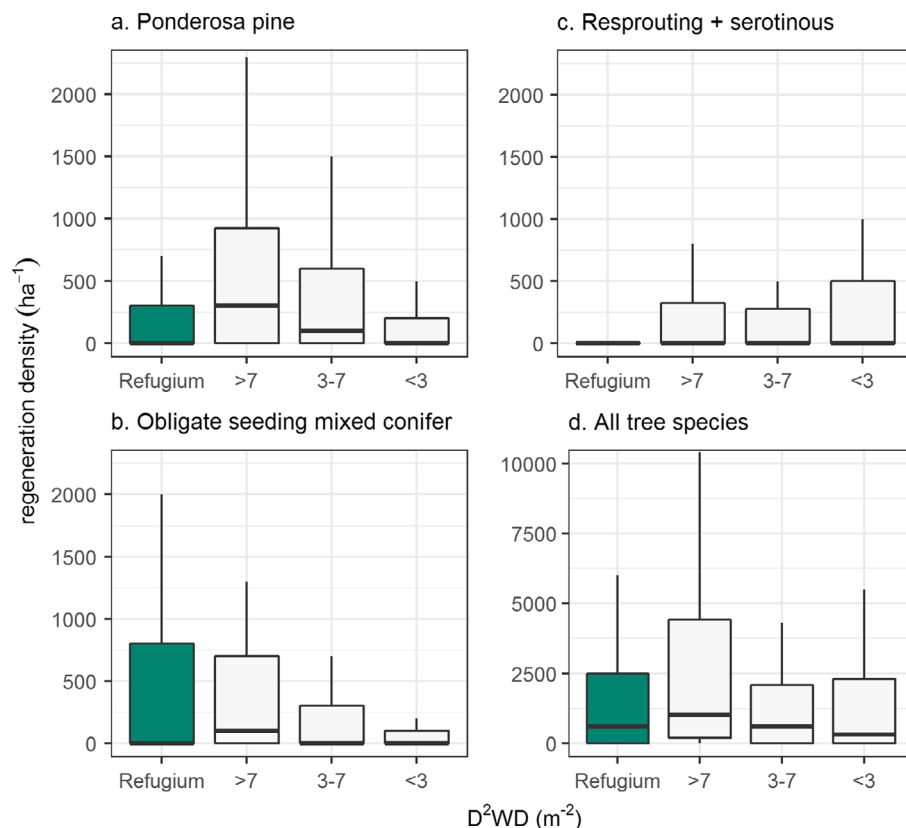


Fig. 4. Regeneration densities within refugia (green, leftmost bar in each graph) and burn interiors (gray bars) as a function of decreasing distance-weighted refugium density. D^2WD is the distance-weighted density of fire refugia. Tree regeneration assemblages are as follows: (a) ponderosa pine; (b) obligate-seeding mixed-conifer species (all species excluding ponderosa pine, aspen, lodgepole pine, and alligator juniper); (c) resprouting and serotinous species including aspen, lodgepole pine, and alligator juniper; and (d) all tree species.

burned areas outside of refugia ($3066 \pm 6899 \text{ ha}^{-1}$) was comparable to that within refugia, as was frequency, with 77% of plots containing at least one tree seedling. In the northwestern study sites, 16% of non-forest plots lacked tree regeneration; in the southwest, 26% of severely burned plots lacked any tree regeneration. When tree regeneration by all species in was considered, there was a clear peak in abundance within 10 m of refugia and where D^2WD was greatest (Figs. 3d, 4d).

Field-derived relationships between refugium pattern and forest recovery

Generalized linear mixed-effects models revealed strong relationships between tree

regeneration, distance (D), distance-weighted refugium density (D^2WD), and burn identity, for most species assemblages (Tables 3, 4). Specifically, for all models of the ponderosa pine, obligate-seeding mixed conifer, and all tree species assemblages, the null hypothesis of no effect of refugium density and proximity was rejected. For the resprouting and serotinous species assemblage, the null hypothesis was rejected for the model of raw tree regeneration (seedling and sucker) counts, but model fit was poor (Table 3). However, the null hypothesis of no effect was accepted in the second, time-relativized model for this assemblage (Table 4). Of the best fitting models that retained a distance term, simple Euclidean distance to the nearest



Fig. 5. Abundant seedling regeneration near a ponderosa pine refugium within the Pumpkin burn, Arizona. Photo by R. B. Walker.

seed source, rather than distance squared, was the strongest predictor. Most models included both a distance term and a distance-weighted density term. Of the latter, D^2WD calculated for a 30-cell (300-m) radius was consistently a much stronger predictor than any of the non-squared or lower-radius terms (Tables 3, 4). The random effect term, burn identity, was included in all best fitting models. Variance accounted for by the random effect term was generally least for models predicting regeneration by ponderosa pine and by all tree species combined, and highest for the resprouting and serotinous species group (Tables 3, 4).

Model intercepts and coefficients varied considerably between different species groups (Tables 3, 4), and between models predicting measured vs. time-since-fire relativized seedling

counts (Table 3 vs. Table 4). Ponderosa pine models included both a negative D term and a positive D^2WD term. Obligate-seeding mixed-conifer seedling counts were best predicted by D and D^2WD (Table 3), but only D^2WD for time-relativized counts (Table 4). Models of resprouting and serotinous species counts also retained a marginally non-significant negative distance term ($P = 0.07$) but showed a negative relationship with D^2WD . However, the best model of time-relativized counts of resprouting and serotinous species regeneration excluded both spatial terms and included only the random effect of burn identity (Table 4). Finally, models of regeneration for all tree species had higher modeled intercepts and included both D and D^2WD term for raw counts (Table 3) but only D^2WD for time-relativized counts (Table 4).

Landscape simulation model findings

Simulation model outputs exhibited contrasts between different species assemblages, but also illustrated several shared patterns (Fig. 6; Appendix S1: Figs. S1, S2). Three models, for ponderosa pine, obligate-seeding mixed conifer, and all tree species combined, showed strongly increasing, but non-linear, landscape recovery (x axes, Fig. 6a, b, d) with increasing proportion of the landscape occupied by refugia (y axes) and over time. Smaller patches contributed disproportionately to tree regeneration—for any given proportion of the landscape occupied by refugia, small refugia promoted recovery over a greater

area (Fig. 6a, b, d). The model for our resprouting and serotinous assemblage (Fig. 6c) was distinct in that these species were not associated with refugia.

Ponderosa pine and mixed-conifer models differed slightly in the position of the y -intercept: For landscapes with an initial refugia proportion of zero, the mixed conifer models (Fig. 6b) indicated some regeneration still occurred, whereas ponderosa pine models (Fig. 6a) did not. Our model that combined all tree species (Fig. 6d) showed substantially elevated forest recovery compared with the ponderosa pine and mixed-conifer models due to the contributions of

Table 3. Generalized linear mixed-effects model intercepts, coefficients, significance, and overdispersion (θ) parameters for relationships between refugium neighborhood metrics (D , Euclidean distance; D^2WD , distance-squared weighted density within a 300-cell radius moving window) and tree regeneration counts.

Variables	Intercept	Fixed effects coefficients		Random effect		AIC	Marginal R^2_{GLMM}	Conditional R^2_{GLMM}
		D (m)	$D^2\text{WD}$ (m^{-2})	(Variance) Burn	θ			
Ponderosa pine	0.365	−0.004**	0.162***	1.515	0.36	2292	0.32	0.91
Obligate-seeding mixed-conifer species	0.471	−0.013***	0.087**	5.296	0.35	1839	0.22	0.98
Resprouting + serotinous species	1.333	−0.005†	−0.122**	8.217	0.18	1934	0.02	0.99
All tree species	2.436***	−0.003*	0.079***	2.277	0.48	3622	0.09	0.90

Notes: AIC, Akaike's information criterion. Tree regeneration models are as follows: ponderosa pine; obligate-seeding mixed conifer (all species excluding ponderosa pine, aspen, lodgepole pine, and alligator juniper); resprouting and serotinous species (including aspen, lodgepole pine, and alligator juniper); and all tree species. All models employ a negative binomial family with 493 observations.

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4. Generalized linear mixed-effects model intercepts, coefficients, significance, and overdispersion (θ) parameters for relationships between refugium neighborhood metrics (D , Euclidean distance; D^2WD , distance-squared weighted density within a 300-cell radius moving window) and time-since-fire relativized tree regeneration counts.

Variables	Intercept	Fixed effects coefficients		Random effect		AIC	Marginal R^2_{GLMM}	Conditional R^2_{GLMM}
		D (m)	$D^2\text{WD}$ (m ⁻²)	(Variance) Burn	θ			
Ponderosa pine	−1.949***	−0.006†	0.140***	0.551	1.07	762	0.30	0.49
Obligate-seeding mixed-conifer species	−3.139***		0.179***	4.199	1.06	684	0.10	0.82
Resprouting + serotinous species (<i>intercept only</i>)	−1.992**			5.957	0.58	882	0.00	0.92
All tree species	−0.445		0.097***	1.807	0.89	1581	0.06	0.72

Notes: AIC, Akaike's information criterion. Tree regeneration models are as follows: ponderosa pine; obligate-seeding mixed conifer (all species excluding ponderosa pine, aspen, lodgepole pine, and alligator juniper); resprouting and serotinous species (including aspen, lodgepole pine, and alligator juniper); and all tree species. All models employ a negative binomial family with 493 observations. Empty cells indicate the term was not included in the best fitting model.

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

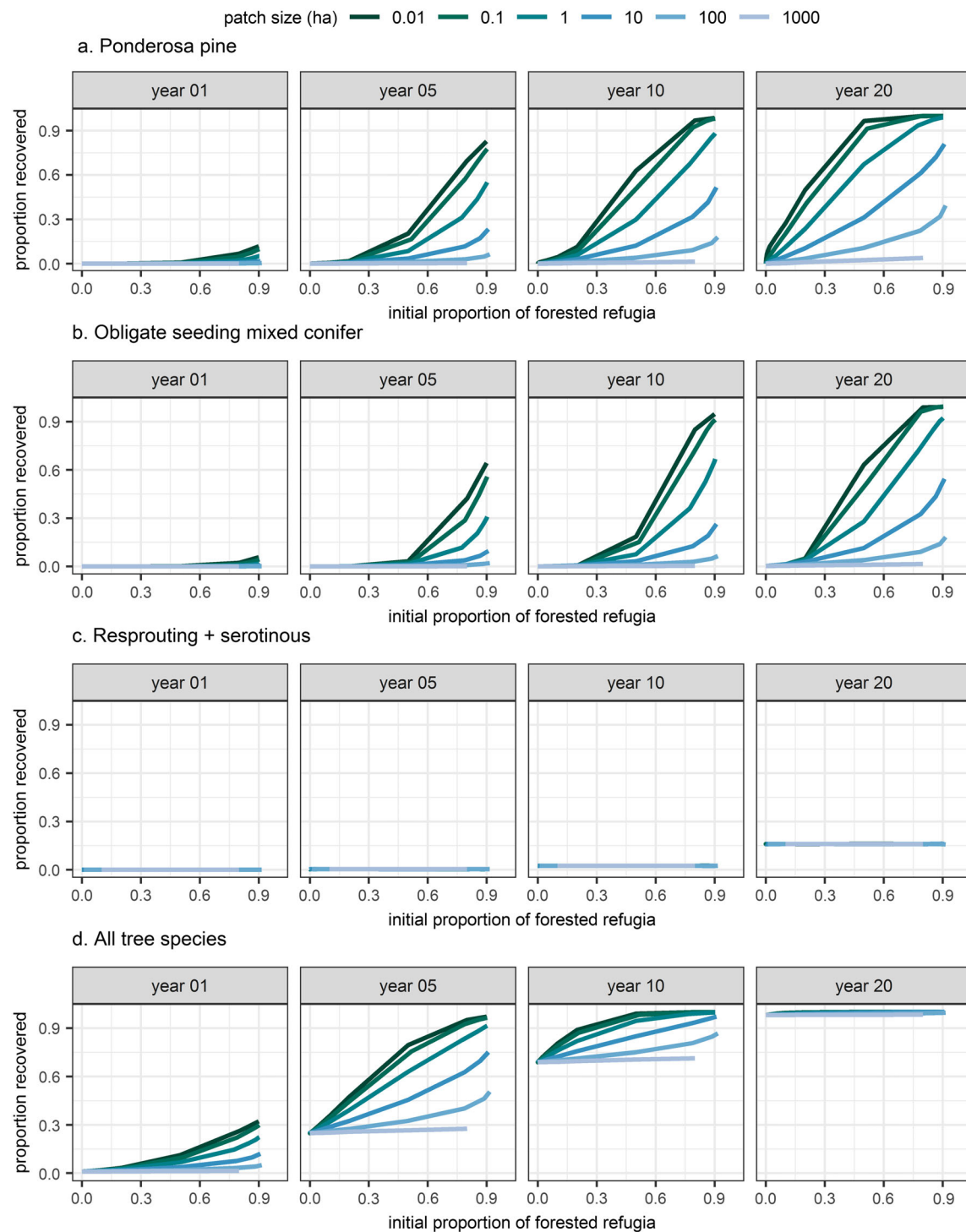


Fig. 6. Simulated regeneration of (a) ponderosa pine, (b) obligate-seeding mixed-conifer species, (c) resprouting and serotinous species, and (d) all tree species over time as a function of refugium patch size and landscape proportion. Here, a moderate value of ≥ 5 individuals/pixel (500 ha^{-1}) is used as a threshold by which non-forested cells were deemed recovered (thresholds of ≥ 1 and ≥ 10 are illustrated in Appendix S1: Figs. S1, S2).

species not dependent on live tree seed sources. However, this model also displayed comparable patterns of increasing forest recovery with greater initial abundance of refugia, increasing recovery over time, and disproportionate effects of small patches.

DISCUSSION

Fire refugia promote forest resilience

Fire refugia shape spatial resilience of forest landscapes by promoting tree recovery within high-severity burns across study sites spanning the interior western United States. For a range of tree species, seedling abundance is closely linked to the proximity and neighborhood density of refugia, which can be modeled as a composite, distance-weighted density (D^2WD) metric. Simulations also revealed that, for any given landscape proportion, small refugia contribute to disproportionately greater recovery than larger patches.

Notably, the greatest regeneration of ponderosa pine, the dominant tree species within our study system, occurs in areas of stand-replacing fire immediately adjacent to surviving tree seed sources. These findings illustrate the dependence of regeneration on the nearby live seed sources (Chambers et al. 2016, Owen et al. 2017) and perhaps also support the beneficial role of fire in promoting ponderosa pine seedling establishment via decreased competition for both above- and below-ground resources (Harrington and Kelsey 1979, Bonnet et al. 2005). Somewhat in contrast, regeneration by other obligate seeders in the mixed conifer assemblage, composed primarily of Douglas-fir and true firs, was greatest within refugia; these species appear to benefit from their relatively high shade tolerance (Oliver and Dolph 1992), but regeneration diminishes rapidly with decreasing proximity and density of seed sources.

Our results demonstrate that relationships between distance to live tree seed sources and post-fire regeneration by ponderosa pine and mixed-conifer tree species (Bonnet et al. 2005, Haire and McGarigal 2010, Chambers et al. 2016, Kemp et al. 2016, Rother and Veblen 2016, Owen et al. 2017) can be extended to predict regeneration across a continuum of seed-source patch sizes and densities, including

small and island-like refugia. These are frequently $<100\text{ m}^2$ (R. B. Walker, *unpublished data*) and may be difficult to detect using 30-m resolution satellite imagery. Though easily overlooked, such locations can serve as essential catalysts of recovery deep within burn interiors where propagule sources are otherwise lost and forest recovery compromised.

While a broad definition of resilience might allow for recovery to a different composition of tree species, a narrower application of the concept requires the recovery of pre-disturbance structural and compositional attributes (i.e., a forest of the same species that occurred prior to fire). Together, ponderosa pine and the species composing our mixed-conifer assemblage account for the vast majority of individual trees and basal area within sampled refugia, and by extension, likely pre-fire composition. However, within some study burns we also observed substantial contribution to forest recovery by resprouting and serotinous species. Our statistical models for this assemblage do not point toward clear and consistent relationships between their patterns of recovery and the local availability of live tree seed sources. Work elsewhere has demonstrated that the regeneration of species displaying alternate regeneration strategies well suited to stand-replacing fire is generally unlinked to proximity to live seed sources (Coop et al. 2010, Harvey et al. 2016, Kemp et al. 2016). Aspen and lodgepole pine collectively accounted for only a very small proportion of the total basal area and number of individual trees ($<1\%$) within sampled refugia but contributed disproportionately to regeneration in severely burned sites. However, their regeneration was highly variable—generally occurring as high-density patches or absent. These species are rarely important components of ponderosa pine and dry mixed-conifer forest types; instead, both species often form extensive mono-dominant forests with infrequent, stand-replacing fire at higher elevations (Peet 1981). Where they intergrade into the burned ponderosa pine and dry mixed-conifer forests of our study, their contribution to post-fire reforestation is pronounced. Abundant regeneration by these species might lead to the recovery of forest but of an alternate composition (e.g., aspen). However, despite their influences, when all tree species are considered

together, regeneration still showed strong spatial dependence on fire refugia.

The fire refugia we sampled in most cases exhibited evidence of exposure to wildfire (in the form of scorched boles and char) that burned nearby areas at much higher severity. Stochastic variation in fire behavior can shape the post-fire mosaic of unburned and burned patches. However, because our sampled refugia were clearly exposed to fire but were only lightly affected, we posit that they generally possessed at least some degree of fire resistance. Identifying the causes of this resistance was beyond the scope of our research, but it may be attributable to intrinsic structural characteristics such as the low tree density and high crown base heights we frequently observed in these locations, which would limit active crown fire spread and reduce transitions from surface to crown fire (Scott and Reinhardt 2001). Alternately, resistance may be a product of disturbance history on landscape fuel continuity (e.g., influences of prior wildfires; Parks et al. 2015), or extrinsic topographic factors that limited fire spread for example proximity to natural fuel breaks such as a rock outcropping (Parisien et al. 2011, Krawchuk et al. 2016).

Our findings point toward an interplay between resistance and resilience, with implications for the spatial resilience of landscapes. Fundamentally, disturbance-resistant settings (fire refugia) can entrain resilience (forest regeneration) elsewhere across the landscape. Relationships between resistance and resilience can be illustrated with ball-and-cup diagrams representing stability landscapes, which are in turn linked to locations on the physical landscape (Fig. 7). In this conceptualization, local-scale resistance promotes landscape-scale resilience essentially by tilting the stability landscape. A return toward dominance by obligate-seeding ponderosa pine and other conifers is favored where the degree of tilt is greatest, and hindered where tilt is least, and where transitions to alternate forest (i.e., aspen or lodgepole pine) or non-forest types are most likely. Within our study system, the increase in resilience (or positive inclination of the stability landscape) rises as a function of refugium proximity and abundance, which are relatively easily quantified as distance and neighborhood density (D^2WD). As such, this relatively simple metric may have utility in efforts

to measure spatial resilience of landscapes (Peterson 2002). The influence of local-scale processes on landscape-scale resilience illustrated here also complements prior work emphasizing broader-scale influences on resilience at finer scales (Nyström and Folke 2001).

Insights from statistical and simulation models

Statistical models demonstrated strong relationships between tree regeneration and our distance-weighted refugium density (D^2WD) metric. Numerous studies have highlighted the predictive capacity of seed-source distance on regeneration by wind-dispersed, obligate-seeding North American conifers (Bonnet et al. 2005, Coop et al. 2010, Chambers et al. 2016, Kemp et al. 2016, Rother and Veblen 2016, Owen et al. 2017), and this metric may be of high utility for natural resource managers for whom a threshold distance necessary for natural forest recovery could provide a useful rule of thumb for reforestation efforts. However, propagule availability is generally not a linear function of distance (Clark et al. 1998, Haire and McGarigal 2010, Landesmann and Morales 2018, Downing et al. 2019). Our D^2WD term that integrated potential seed rain from multiple sources was generally a much stronger predictor of tree regeneration than linear distance (Tables 3, 4). The squared distance term in this metric meant that values decreased geometrically away from seed sources, consistent with the expectation that seed rain declines non-linearly across two dimensions. In all models, the strongest D^2WD term was also that calculated at the largest, 300-m radius, window. For many sites, we were constrained from using larger window sizes as they would have extended beyond mapped burn perimeters. However, increasingly robust relationships with increasing radius suggest that even larger window sizes could potentially serve as stronger predictors. Interestingly, several models included both simple distance (D) and D^2WD terms. This finding, implying that both metrics provide some independent information, leads to two possible interpretations. First, the distance term (which was not constrained to a particular window size and was occasionally >300 m) may have retained utility at distances beyond 300-m radius limitation on the window size of D^2WD . Alternatively, seedling counts may not have declined as

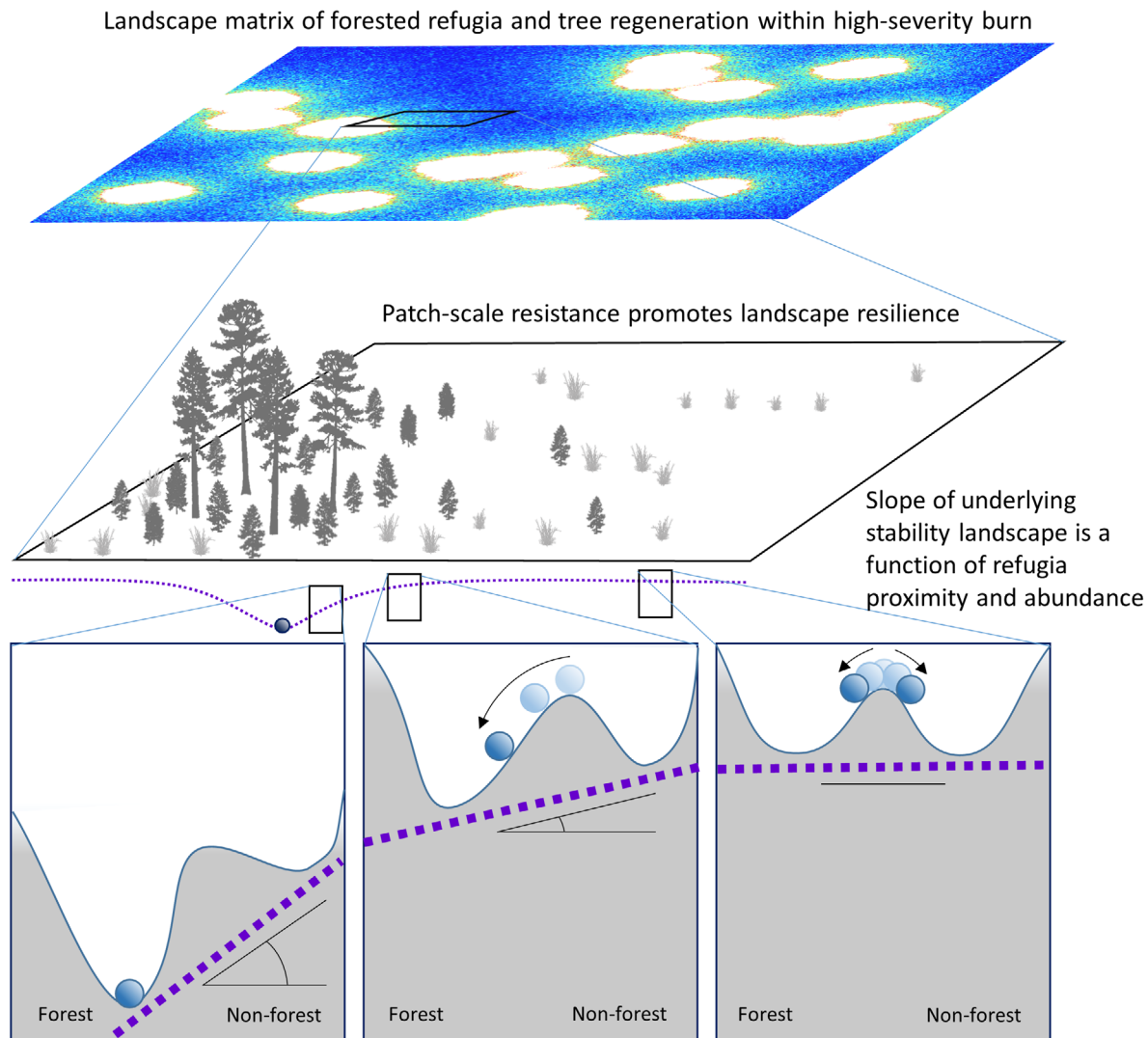


Fig. 7. Patch-scale fire resistance confers resilience at a broader scale on the physical landscape by bending the underlying stability landscape. The angle of the stability landscape (dashed violet line) increases as a function of refugium proximity and abundance on the physical landscape. A return to a forested state is favored where the inclination is greatest (where refugia are close and abundant) and impeded where it is least (where refugia are distant and sparse).

abruptly with distance as the squared D^2WD term due to some mechanism of self-inhibition such as shading, operating over narrow spatial scales adjacent to refugia.

Simulation models of forest recovery for dominant, obligate-seeding trees reveal several important facets of the relationship between refugia and post-fire recovery. Most notably, for any given landscape proportion of refugia, small refugia

contribute to disproportionately greater landscape reforestation than larger patches. Furthermore, the landscape proportion of refugia within burn perimeters may not matter as much as their size and abundance. This finding strongly supports work emphasizing small-scale patchiness as a key to landscape resilience in dry forest types (Churchill et al. 2013). The smallest patch size represented in our model was 0.01 ha, but a

logical extension of the relationships we elucidated suggests that landscapes consisting of even smaller patches—perhaps as small as one tree in size—would promote even greater regeneration. Interestingly, the maintenance of such small-scale patchiness would have required extensive and frequent fire, lethal to tree seedlings but not adults, to prevent rapid canopy infilling, which is consistent with our understanding of pre-settlement fire regimes and their effects in these systems (Allen et al. 2002). On the other hand, our model findings suggest that a landscape composed of very large patches of forest and non-forest would be the least dynamic and most stable, exhibiting slow infilling of non-forest patches. The maintenance of such a landscape pattern would require less frequent disturbance.

Simulation models also demonstrate non-linear relationships between refugium abundance and the extent and rate of post-fire forest recovery, with most showing inflections near 50% cover by forested refugia (Fig. 6). The actual proportion of forested refugia retained at our study sites ranged from 20% in the Hayman burn to 57% in Poplar (R. B. Walker, *unpublished data*). However, the general shape of these relationships depends somewhat on our criterion for recovery. Given expected seedling mortality, Ouzts et al. (2015) suggest that a ponderosa pine seedling density of 125–240 ha⁻¹ would be necessary to produce a density of mature trees within the historical range of variation of 55–106 ha⁻¹. To put these values in perspective, residual mean tree density within sampled refugia was 314 ha⁻¹ for all species but averaged 137 ha⁻¹ for ponderosa pine. As such, the threshold value of ≥ 5 stems per cell (500 ha⁻¹; Fig. 6) represents a moderately conservative criterion of post-fire regeneration by this species. For a recovery threshold of ≥ 1 stem per cell (displayed in Appendix S1: Fig. S1; 100 seedlings/ha), ponderosa pine and obligate-seeding mixed conifer assemblage models show plateauing recovery at refugium percentages more than ~50% within 10 yr post-fire. In contrast, when a higher recovery threshold (≥ 10 stems per cell; 1000 ha⁻¹; Appendix S1: Fig. S2) was applied, models indicated sparse or no recovery across landscapes with less than ~50% refugium cover, with rapid increases at greater proportions. Finally, our findings also highlight that in forests containing species such as aspen

and lodgepole pine, forest recovery following high-severity fire is also enhanced away from refugia. Long-term, post-fire landscape composition and pattern will necessarily reflect the both the template provided by a mosaic of disturbance effects and the influences of species adaptations.

Implications for conservation and management of vulnerable forest landscapes

Our study demonstrates the important role of fire refugia in the post-fire landscape recovery of forest systems considered vulnerable to changing fire regimes. Our findings also contribute to a growing body of work highlighting the value of refugia more generally for the conservation of biota and maintenance of essential ecological processes in a time of intensifying environmental change (Keppel et al. 2012, 2015, Hannah et al. 2014, Reside et al. 2014). These findings lead to a number of management implications and applications. In particular, fire and forest managers in the western United States are tasked with fostering resilient landscapes (Wildland Fire Executive Council 2014). We encourage conservation practitioners and managers to explicitly consider the potential role and configuration of fire refugia in promoting resilient forest systems prior to wild-fire, during incident management, and in the post-fire landscape.

In addition to continuing to develop an understanding of the capacity for landscapes to harbor refugia, management activities could be used to maintain existing refugia or promote refugia formation during disturbance. Topography, microclimate, and burn-severity models, along with field data, can be used to gain pre-fire insight into the potential for landscapes to support fire refugia (Haire et al. 2017), particularly persistent refugia with old-growth forest attributes (Rogean et al. 2018). Such refugia may be essential for the conservation of particular species (Schwilk and Keeley 2006, Swengel and Swengel 2007), and where fire refugia are the product of cooler microclimates, these locations may also buffer species against climate change (Wilkin et al. 2016). However, the formation of transient refugia, not necessarily linked to topographic features, but instead to vegetation structure or fuel breaks, could be promoted via fuel reduction treatments applied to generate fire-resistant islands within a matrix of areas more susceptible

to crown fire. Increases in forest retention through fire may be achieved with relatively minor, but strategic, configuration of treatments (Ager et al. 2010). Our findings suggest that treatments promoting the retention of abundant pockets of surviving trees (as small as 0.01 ha), rather than fewer, larger stands, best facilitate natural post-fire reforestation. Fire incident management may also provide opportunities to encourage the formation of refugia by, for example, shifting patterns of suppression or burnout activities, or promoting fire under conditions most likely to yield desired landscape pattern. Fires burning under moderate conditions best allow for topographic factors to shape heterogeneity of burn effects, including abundant and predictable fire refugia (Krawchuk et al. 2016).

Our results may also guide post-fire vegetation and fuel management. First, they highlight the value of fire refugia for natural forest regeneration and provide some suggestions for conserving fire refugia through time. Identifying, mapping, and determining the species composition of these refugia may require field surveys and analysis of high-resolution and/or multi-spectral imagery (Meigs and Krawchuk 2018). Because landscapes are dynamic, these patches may also be worthy of subsequent efforts to reduce fuel accumulations (including heavy dead and down fuels produced by fire, and post-fire regrowth). Abundant tree regeneration around the margins of refugia may, in a few years, result in vertical fuel continuity that could make refugia vulnerable to transition from ground fire to crown fire. Second, managers may be able to leverage natural tree regeneration emanating from refugia by targeting replanting efforts away from these sources. Metrics like D^2WD could help identify locations least likely to regenerate naturally. Additionally, where forest recovery is a high priority but refugia are scarce and resources for replanting are limited, plantings could be configured to create small islands (i.e., applied nucleation; Corbin and Holl 2012) that could ultimately provide the form and function of refugia.

Study limitations, opportunities, and conclusions

Our focus here on general relationships between spatial proximity and density of refugia and post-fire landscape dynamics precluded

more detailed consideration of a suite of other biotic and abiotic factors well known to mediate post-fire tree regeneration, all of which could be examined in future work. As one example, our model does not incorporate influences of topography or directionality, both of which influence dispersal of wind-dispersed seeds. As another, we have not investigated whether refugia owing their origins to fundamentally different processes (persistent topographic features, more dynamic shifts in vegetation structure and fuels, or less predictable nuances of fire behavior) might vary meaningfully in composition and function. Importantly, the random effect term included in our statistical models (burn location) was significant in all models. High variability in regeneration densities between burns is likely attributable to climate means and variation, but may also be imparted by substrate, competing/facilitating vegetation types, and many other factors. In particular, the effects of climate on post-fire tree seedling establishment (Haffey et al. 2018, Stevens-Rumann et al. 2018) will substantially modulate the function of fire refugia and warrant more detailed examination. In the work presented here, our simulation models were parameterized using essentially the average effect of refugia across all 12 burns, which mask considerable variation between landscapes with very sparse tree regeneration and those where tree seedlings were abundant. Such burn-specific effects could also be applied to spatially predict regeneration patterns within any given site. We also note that the refugium maps (from which models were derived) do not provide data on tree species composition, and our simulations incorporate tree species occurring over a broad geography. As such, these models necessarily gloss over important influences of tree species composition and are not necessarily representative of any given site. Additionally, species other than ponderosa pine were modeled as assemblages based on expected dependence on live tree seed sources, which may further obscure important species-specific variation in post-fire ecology (e.g., aspen and lodgepole pine; Whitman et al. 2018).

A key assumption of our simulation model was that regeneration continued over a 20-yr time frame. Field counts of branch internodes of ponderosa pine seedlings, which correlated

strongly with counts of tree rings, indicated ongoing regeneration throughout the interval between fire and our sampling (Downing et al. 2019)—a finding consistent with studies examining even longer intervals (Savage and Mast 2005, Shatford et al. 2007, Haire and McGarigal 2010). Our model also considered average annual recruitment for all species, even ponderosa pine, which is well known to be highly episodic (Petrie et al. 2016). However, by averaging out inter-annual variation over 12–17 yr post-fire, and applying the simulation over a comparable time frame, we believe our model inferences to be fundamentally correct.

While we found clear positive effects of fire refugia on tree recovery in burned landscapes, we know little about how these patches contribute to the resilience of other components of biodiversity and the maintenance of a range of ecological and evolutionary processes. The development of such an understanding will benefit from a wealth of earlier work on metapopulation dynamics, landscape ecology, island biogeography, and phylogeography, but will also require new research specific to emerging questions in the context of changing fire regimes and climate. Though we found small refugia were disproportionately important for tree regeneration, the conservation of particular species and the maintenance of certain ecological processes may benefit from larger patches or exhibit complex multi-scalar patterns. For example, in our study burns in the southwestern United States, the tassel-eared squirrel (*Sciurus aberti*) is an arboreal mammal dependent on live ponderosa pine basal area and canopy cover at local and landscape scales (Prather et al. 2006). Where refugia possess uncommon attributes such as old-growth forest structure, they may also harbor species adapted to those conditions. In Australia, fire is less frequent and/or severe in gullies than the surrounding landscape, which maintain greater forest structural complexity (Collins et al. 2012) and diverse bird communities (Robinson et al. 2016). Consistent with the species-area relationship, Adie et al. (2017) found that tree species richness increased as a function of fire refugium area in South Africa. Refugia may also maintain genetic diversity and shape the spatial genetic structure of populations of organisms in fire-prone landscapes (Banks et al. 2017).

Our findings contribute to a broader understanding of the general role refugia may play in the conservation of biota and maintenance of ecological processes (Keppel et al. 2015). Refugia represent change-resistant outposts that hold promise in seeding resilience to anthropogenic environmental change across a range of terrestrial and aquatic systems. To what extent can refugia be identified in advance of impacts, how well might their spatial and temporal dimensions correspond with anticipated conservation demands, and how might their function be maintained or degraded by human influences? Answering such questions may be particularly relevant given accelerating shifts in climate and disturbance and their impacts across a diversity of ecological systems, from forests (Allen et al. 2010) to coral reefs (Hughes et al. 2003).

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