



UN DECADE ON ECOSYSTEM RESTORATION

RESEARCH ARTICLE

Identifying priorities for post-fire restoration in California chaparral shrublands

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When wildfires occur at sufficiently low frequencies, chaparral shrubland regenerates without the need for active restoration. However, shrubland with high fire frequency, particularly in conjunction with other stressors, can require active restoration. Here we present a Post-fire Restoration Prioritization (PReP) tool for chaparral shrublands which identifies priorities for post-fire restoration based on the regeneration potential of shrubs and accounts for fire history, drought tolerance, and competition from annual grasses. We demonstrate the tool on the Copper (2002) and Powerhouse (2013) fires on the Angeles National Forest and determine that 9% (665 ha) and 14% (1,532 ha) of the fire areas, respectively, have low regeneration capacity, and therefore represent priority areas for restoration. For more recent fires (≤ 2 years ago), an additional component of the tool integrates erosion risk data to identify locations where active restoration may enhance hillside stabilization. To ground-truth tool outputs for the Powerhouse Fire, we sampled 57 plots to assess if recovery was indeed impeded in low versus high regeneration capacity classes. Low regeneration plots exhibited significantly higher grass and herbaceous cover, with high abundance of non-native species. Furthermore, resprouting shrub species contributed proportionally more cover than obligate seeders in low regeneration plots, with fewer individuals regenerating from seed compared to resprouting. These findings underscore the potential of the PReP tool to provide credible spatial guidance for shrubland management, both in California and potentially in other Mediterranean-type climate regions, as to where active restoration is most likely to ensure long-term sustainability of chaparral and associated ecosystem services.

Key words: drought, ecosystem services, erosion, national forests, non-native species, resource management, southern California, wildfire

Implications for Practice

- The Post-fire Restoration Prioritization (PReP) tool provides a tool for resource managers to prioritize areas for active restoration within vast burned areas of chaparral shrublands.
- The science-based tool integrates a variety of stressors that impede shrubland recovery to identify areas that have the lowest capacity for natural regeneration.
- The tool can be readily applied to any shrublands in southern California, and potentially to shrublands in other Mediterranean-type climate regions.

shrublands (Keeley & Safford 2016), however, the average and maximum size of fires has been increasing over the last two decades (Van de Water & Safford 2011; Pratt et al. 2014; Safford et al. 2018). Seven teen fires have burned more than 40,000 ha in southern California: nine of these have occurred since 2000 and 14 since 1970 (USDA 2019), many of which have occurred in chaparral shrublands.

Author contributions: HS conceived of idea to develop tool with EU; EU, AH worked to create the tool and compiled input data with guidance from HS, NM; LL, NM designed field data collection; data were analyzed by LL, NM; EU led writing of manuscript with contributions from NM, LL, HS.

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Introduction

The national “forests” of southern California—the Angeles, Cleveland, Los Padres, and San Bernardino National Forests (Fig. 1)—are ironically dominated by shrublands, primarily chaparral: an evergreen, hard-leaved ecosystem that grows generally on low productivity soils in sites prone to periodic fire (Rundel 2018). Wildfire is a natural process in chaparral

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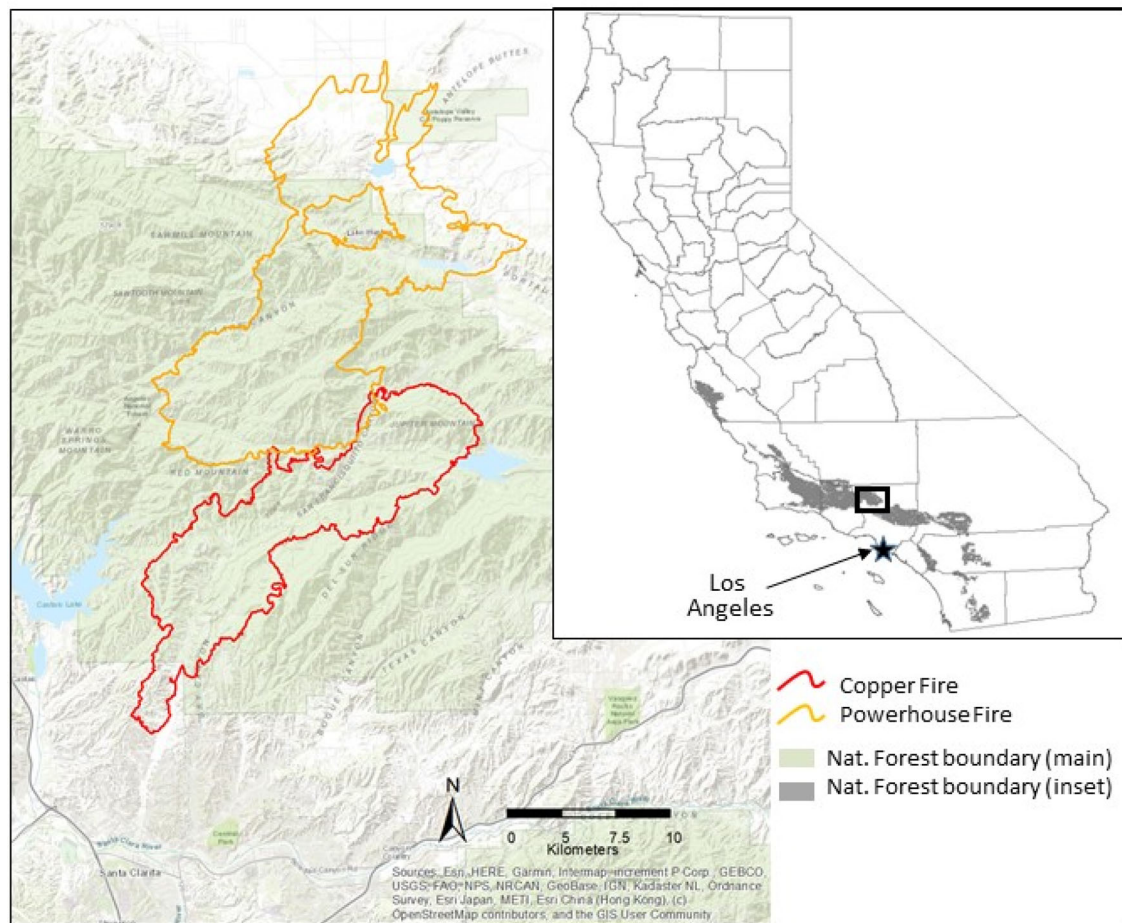


Figure 1. Locator map of the Copper and Powerhouse fires on the Angeles National Forest. Inset map shows distribution of the four shrubland-dominated forests in southern California.

Too frequent wildfire results in chaparral degradation and alters the provision of ecosystem services (Underwood et al. 2018; Syphard et al. 2019), which has led the USDA Forest Service to restore burned chaparral landscapes. Restoration post-fire is not only expensive and time-intensive (Kimball et al. 2015; Rohr et al. 2018) but given the sheer scale of shrubland wildfires, the identification of sites for restoration presents a daunting task. To this end, we developed an assessment tool for resource managers underpinned by our best understanding of the mechanisms of chaparral recovery post-fire to identify candidate areas for restoration.

Historically, chaparral has exhibited high intrinsic regeneration capacity following fire (Allen et al. 2018). There are three modes of post-fire shrub recovery (Jacobsen et al. 2007; Pratt et al. 2007; Pausas & Keeley 2014): (1) obligate resprouter species, regenerate solely by resprouting new shoots from dormant buds; (2) obligate seeder species, regenerate through the germination of fire-cued seedbanks and do not resprout post-fire; and (3) facultative seeder species, regenerate through both mechanisms. However, some stressors can impact regeneration sufficiently to require active restoration (Keeley & Brennan 2012). First, the interval between fires is a key consideration: obligate

seeders are particularly susceptible to short interval fire as they regenerate entirely from long-lived, fire-cued soil seedbanks that require one to two decades to replenish (Haidinger & Keeley 1993; Zedler 1995; Keeley & Brennan 2012). Fires at short intervals can eliminate seeders from the community and allow the persistence of ruderal species like non-native grasses and forbs (Syphard et al. 2018). Although resprouting species are more resilient to higher fire frequencies, even resprouter dominated chaparral stands can be converted to grasslands composed of non-native species (Keeley 2006; Syphard et al. 2018).

Second, extreme drought conditions before fire can impact regeneration particularly for resprouting species. Pre-fire drought can reduce the accumulation of biomass and deplete carbon stores (Pratt et al. 2014; Jacobsen & Pratt 2018). This becomes critical during post-fire regeneration, when resprouters draw extensively on carbon reserves to fuel resprouting and maintain their large root systems. For obligate seeders, drought in the years after fire reduces germination and seedling survival (Pratt et al. 2014). Finally, post-fire regeneration is negatively related to the abundance of annual grasses, most of which are non-native from the Mediterranean Basin. Such species threaten obligate seeder shrubs because they compete

for water in shallow soil layers (Phillips et al. 2019), shade out shrub seedlings, and can notably alter the successional trajectory of burned shrublands. This is particularly relevant given that one of the six USDA Forest Service priority goals for the southern California national forests is to reduce impacts from invasive species and restore the health of federal lands (USDA 2004).

In this study, we describe the Post-fire Restoration Prioritization (PReP) Tool (available for download at <https://github.com/adhollander/postfire/>), which identifies priorities for active restoration post-fire by assessing the regeneration potential of native shrubs and accounts for fire history, drought tolerance, and competition from annual grasses. The PReP tool is based on an approach that supports post-fire forest planning in Spain (Alloza et al. 2006; Alloza & Vallejo 2006; Duguy et al. 2012), which we adapted to shrubland dominated landscapes in southern California. We have integrated a novel drought and grass component and created an interactive interface for the tool for resource managers. In this study, we illustrate the utility of the tool using the Copper (2002) and Powerhouse (2013) fires on the Angeles National Forest (ANF). The development of the PReP tool contributes to a growing number of spatial prioritization tools for restoration in the world's four Mediterranean-type climate regions.

Methods

Overview of Post-Fire Restoration Prioritization Tool

The PReP Tool provides a dynamic, repeatable framework for resource managers to guide and prioritize post-fire restoration with the goal of restoring native chaparral. The tool uses a Jupyter notebook framework (Kluyver et al. 2016) to provide an interactive workflow to conduct geospatial computations using a conceptually straightforward scoring method (Data S1). The tool consists of five steps (Fig. 2) and sub-steps (tasks) to determine the relative regeneration capacity of pixels (30 × 30 m) within the fire perimeter. We illustrate the tool using the Copper Fire (2002), which burned 9,500 ha (23,500 acres) in the western portion of the Angeles National Forest, about 60 km northwest of downtown Los Angeles (Fig. 1). We then undertook fieldwork in the Powerhouse Fire (2013, adjacent to the Copper Fire on the ANF) to evaluate whether the projected regeneration capacity outputs of the PReP tool are supported by field data. The Copper and Powerhouse fires are adjacent to each other on the ANF and consist of similar vegetation communities, primarily mixed chaparral with some chamise redshank chaparral and annual grasslands.

Step 1. Determine the Post-Fire Regeneration Potential by Assigning Proportion of Resprouters and Facultative Seeders

Baseline regeneration potential is first assigned based on the proportion of resprouting species, which we defined as resprouters plus facultative seeders (because both reproductive strategies resprout). In the absence of high-resolution vegetation data (and without being able to guarantee resources for fieldwork), we assigned the proportion of resprouters by landscape

units (Mayer & Laudenslayer Jr 1988). Landscape units were based on the California Wildlife Habitat Relations (WHR) classification (Mayer & Laudenslayer Jr 1988) intersected with aspect (two classes: north or south facing) and topography (three classes: summit and ridges, slopes, valleys and depressions; Jasiewicz & Stepinski 2013). These combinations indicate warmer, more exposed WHR vegetation types dominated by seeder species versus cooler, less exposed WHR types which are associated with resprouter species (Gordon & White 1994).

The tool presents a pre-populated table of the percent of surface cover contributed by resprouter plus facultative seeder ("R + FS") species, which a user can modify (the proportion of obligate seeders is the inverse of this value). Data were compiled from an analysis of percent cover of functional groups in USDA Forest Service Forest Inventory and Assessment (FIA) shrubland plots; reference to ecological field guides (Gordon & White 1994; Borchert et al. 2004); and input from botanists (see Table S1). Field surveys are highly recommended to confirm the accuracy of these classes when possible. Based on the proportion of R + FS species within a pixel, we assigned scores to reflect the pixel's regeneration potential as high, medium, or low: pixels with ≥40% R + FS were assigned 4 points (high regeneration class); pixels with 10–40% R + FS 3 points (moderate); and pixels with <10% R + FS 1 point (low, Table S2). For the high regeneration class, the proportion of R + FS is guided by research from Thornes (1995), which considers 30–40% cover to provide effective soil protection to reduce soil erosion. Pixels in the high regeneration class are assumed to have reduced susceptibility to other factors including invasion. The subsequent steps of the tool (steps 2–5) serve to modify the regeneration *potential* points assigned to each pixel by integrating additional data to determine the regeneration *capacity* of each pixel.

Step 2. Modify Regeneration Potential Based on Fire History

The tool integrates two fire history components. First, the number of fires in the previous 40 years. We used a threshold of three or more fires in any given pixel in the 40 years prior to the fire date as the critical number of fires after which species regeneration will be affected (an attribute since 2018 in the USDA Forest Service Fire Return Interval Departure [FRID] geodatabase, Safford & Van de Water 2014; USDA 2019). This is based on the estimated 15 years necessary for seeder species to accumulate sufficient seed for successful post-fire regeneration (Zedler 1995). Note that moister coastal sites may be somewhat more resilient to high-frequency fires. A recent study by Syphard et al. (2018) found fire intervals of ≤10 years represented a critical threshold for shrubland decline and replacement in the Santa Monica Mountains of southern California. If a pixel has had three fires in the last 40 years the regeneration capacity score is reduced by 1 point, and if >3 fires the score is reduced by 2 points (Table S3).

Second, the tool considers the time since last fire in each pixel. Obligate seeders are the most sensitive to time since last fire (TSLF), requiring fire-cued seed germination and a decade or more to replenish seedbanks (Zedler et al. 1983; Lippitt

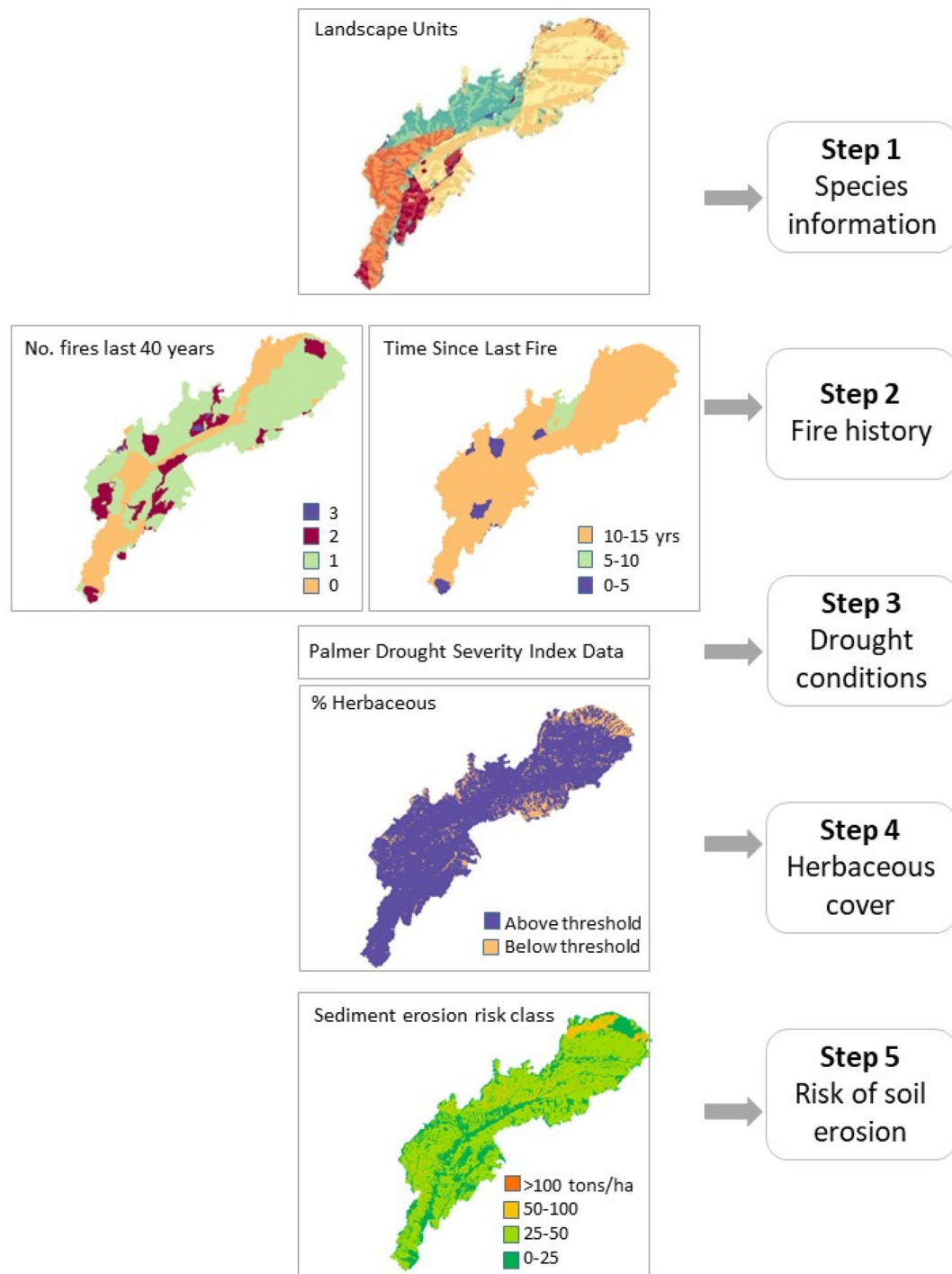


Figure 2. Schematic of steps involved in the PReP tool for chaparral shrublands to determine regeneration capacity of different areas and the input data utilized for the Copper Fire, Angeles National Forest.

et al. 2012). We used TSLF in the Fire Return Interval Departure geodatabase (USDA 2019) and classified values into three classes: 0–5 years, 5–10 years, and 10–15 years (reflecting the importance of TSLF for interior rather than coastal chaparral). For pixels with low regeneration potential (<10% R + FS, i.e.

where S represent 10–90% of shrub cover) and moderate regeneration potential (10–40% R + FS), we reduce the score of pixels, which have 0–5 years TSLF by 2 points and 5–10 years TSLF by 1 point (Table S4); there is no score change where TSLF is ≥10 years.

Step 3. Modify Regeneration Potential Based on Drought

The regeneration capacity incorporates the presence of pre-fire drought and post-fire drought, and also whether the fire occurred in the wet or the dry season. Given the effects of pre-fire drought on the carbohydrate stores of resprouting species (Pratt et al. 2014), this decision rule focuses on adjusting the scores of pixels with $\geq 40\%$ R + FS species (i.e. pixels with high regeneration potential). To inform pre-fire drought conditions, the PReP tool links to a National Oceanographic and Atmospheric Administration (NOAA) website, which calculates the Palmer Drought Severity Index (PDSI) by ecoregion: <https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/>. If ≥ 4 months of the growing season (November to May) in the year before the target fire are “severe” or “extreme” drought (PDSI < -3), the ranking of pixels with $\geq 40\%$ R + FS species is reduced by 1 point (Table S5).

Post-fire drought can affect both the growth of resprouters as well as seedling survival (Pratt et al. 2014) so the decision rule applies to all pixels in the fire scar. The NOAA PDSI website is used to determine if ≥ 4 of the growing season months (November to May) are severe or extreme drought for each of the 2 years following the wildfire (or 1 year, if the tool is being run 1 year post-fire). Modification of the scores of each pixel is made on a cumulative basis, so scores are modified based on year 1 drought conditions first, followed by year 2. Scores are modified using decision trees for either seeder dominated landscape units, that is $< 10\%$ R + FS (low regeneration potential) and $10\text{--}40\%$ R + FS (moderate regeneration potential) (Fig. S1a) or resprouter dominated communities, that is $\geq 40\%$ R + FS (high regeneration potential) (Fig. S1b). The reduction of scores for seeder-dominated pixels is relatively less than resprouter-dominated pixels as research shows seeder species can resist droughts of low to moderate intensity, and droughts over long periods (Pausas et al. 2016).

Finally, studies have shown that wet season (winter) fires occurring in November to May, can reduce fire-dependent seed recruitment, as fires burning over moist soil could lethally heat seeds at or near the soil surface (Beyers & Wakeman 1997). If the fire occurs in the wet season (November–May), then the scores of pixels in the moderate ($10\text{--}40\%$ R + FS) or low ($< 10\%$ R + FS) regenerating classes are reduced by 1 point (Table S6).

Step 4. Modify Regeneration Potential Based on Annual Grass Cover

Competition from annual grasses, many of which are non-natives, is an issue for post-fire shrub recovery (Allen et al. 2018; Syphard et al. 2019). We used available data for 2010 created by Park et al. (2018) which used intra-annual differences in Normalized Difference Vegetation Index (NDVI) from Landsat imagery to differentiate between herbaceous forbs and grasses, which primarily consists of non-native grasses (Franklin 2002), with evergreen shrublands. The percent herbaceous cover for the year before the target fire is integrated automatically into the tool.

As a default, the tool uses a threshold of 20% grass cover in a pixel (threshold can be modified based on field knowledge): above this threshold, grass abundance is considered a high risk to shrub regeneration. For the low ($< 10\%$ R + FS) and moderate ($10\text{--}40\%$ R + FS) regeneration potential classes, that is where seeder species dominate, the scores are reduced by 1 point (Table S7).

Step 5. Integrate Erosion Risk

The final step of the tool integrates the post-fire regeneration capacity and the risk of sediment erosion using four categories: very high, high, moderate, and low, using a matrix modified from the original Spanish tool (Alloza et al. 2016, Table S8). The spatial output of this integration is a map of ecosystem degradation risk. For wildfires occurring > 2 years ago, this output is likely to be the most valuable for informing management decisions, as studies of chaparral in the San Dimas Experimental Forest found 85% of the total sediment delivered over 4 years occurred in the first year post-fire (Wohlgemuth et al. 2009).

The tool integrates data on erosion generated from the USDA Forest Service Burned Area Emergency Response (BAER) assessments, which model the risk of erosion immediately post-fire. For the Copper Fire, erosion data were developed using the USDA Forest Service ERMIT tool (Erosion Risk Management Tool; <https://forest.moscowfsl.wsu.edu/cgi-bin/fswapp/ermit/ermit.pl>) based on the Water Erosion Prediction Program (WEPP) (although note that methods are not standardized between fires). The erosion rate (tons/ha) is modeled relative to an unburned landscape and associated (in this case) with a one in 5-year erosion event (i.e., an exceedance value based on 20% probability). In the PReP tool, modeled data from ERMIT is categorized into four classes based on those used in the original tool from Spain: < 25 tons/ha/year, $25\text{--}50$ tons/ha, $50\text{--}100$ tons/ha, and > 100 tons/ha per year.

Field Validation of PReP Tool Outputs

An important step after running the PReP tool is to conduct on-the-ground monitoring to validate the outputs. We carried out fieldwork using PReP tool outputs for the Powerhouse Fire (2013), which was preferential for fieldwork as it is relatively new compared to the Copper Fire (2002) but has similar vegetation communities and is adjacent (Fig. 1). Field monitoring occurred between June and September 2019. We sampled 57 plots across vegetation type, landscape position, and regeneration capacity class as determined by the PReP tool (Table 1), although restricted access, damaged roads, and challenging topography prevented a fully factorial sampling design. Regeneration capacity classes were determined using the post-fire reproductive strategy, fire history, and competition from annual grasses; we did not, however, include drought in this stratification so as to maximize the range of regeneration classes available to sample in the field.

To validate the utility of the PReP tool on the ground we posed the following questions to assess if recovery is indeed being impeded in low versus high regeneration capacity classes:

Table 1. Fifty-seven field monitoring plots were established six years following the Powerhouse Fire. Plots were established across the four regeneration capacity categories (high, moderate, moderate-low, low), as well as different vegetation types and topographic positions. Note, no areas were categorized as moderate-high.

Landscape Unit		High	Moderate	Moderate-Low	Low
<i>Vegetation type</i>	<i>Aspect and slope</i>				
Mixed chaparral	South facing slopes, summits, ridges	11	—	—	—
Mixed chaparral	North facing slopes, valleys, depressions	11	—	—	—
Chamise Redshank Chaparral	South facing slopes, summits, ridges	—	5	6	7
Chamise Redshank Chaparral	North facing slopes, valleys, depressions	—	7	5	—
Annual Grassland	South facing slopes, summits, ridges	—	—	—	—
Annual Grassland	North facing slopes, valleys, depressions	—	—	—	5

(1) does the cover of grasses, herbs, and shrubs vary by regeneration class? Our assumption is that low regeneration plots would have a higher cover of grasses and herbs, particularly non-native annual species, and a lower cover of native shrubs; and (2) does the proportion of shrubs that regenerate from seeders versus resprouters vary by regeneration class? Note, the data used to address these questions were acquired 6 years following fire and no pre-fire data were available. Therefore, we make the assumption that post-fire data is sufficient for determining recovery or degradation, but we acknowledge that other factors besides the Powerhouse Fire could have contributed to the current vegetation conditions.

Field Measurements. Two field monitoring methods were used: (1) point-line-intercept along a 30-m transect to measure plant species cover and height, and (2) a 30 m² belt transect to determine shrub density. Along the 30 m transect, substrate (bare-ground, litter, rock) and species presence were recorded at 100 points. We recorded the occurrence of multiple species from the same lifeform (grass, herb, shrub) at a single point, which allowed for the calculation of a relative cover value that represents true cover (adjusted for layering and not to exceed 100%) for each lifeform. The covers of resprouting and seeding shrubs were also computed as relative cover. Average height was measured from the soil surface to the top of the tallest branch on at least five individuals per species along the transect line or for all individuals intersected by the line, if fewer than 5. Within the belt transect, we counted all living shrub individuals to determine density.

Species were assigned to three lifeform classes (grass, herb, and shrub) using the Jepson Flora Project (2020). Shrubs were further binned based on their capacity to resprout (R and FS were combined into a “resprouting” category), based on published literature and online databases (FEIS n.d.; Gordon & White 1994; Borchert et al. 2004) and expert opinion. All shrub species were native.

Data Analysis. To understand the relationship between the regeneration capacity class and lifeform cover, we ran analysis of variance (ANOVA) models with % relative cover of grass, herb, and shrub by regeneration capacity class. We analyzed the data using coarse landscape (vegetation) units (i.e., without

aspect or topography). We excluded annual grassland from the analysis because it was not represented across multiple regeneration capacity classes and pre-fire it was mapped as being devoid of shrubs. However, we tested for sensitivity by repeating the above analysis with the annual grassland vegetation type included. We also performed a two-way ANOVA with topographic position and vegetation type to determine its effect on lifeform cover. We assumed landscape position may affect recovery due to differential species composition and productivity on north-facing slopes, valleys, and depressions compared to south-facing slopes, summits, and ridges. Herbaceous species cover was natural log transformed to meet the assumptions of ANOVA and a Tukey HSD post-hoc analysis was used to distinguish differences between regeneration capacity classes.

To evaluate the relationship between regeneration capacity and regeneration strategy (resprouter, seeder) we compared the cover, density, and height of shrubs across regeneration classes. We used two-way ANOVA to evaluate the effects of regeneration capacity class and regeneration strategy on relative shrub cover, total density, and height. We conducted this analysis separately for chamise redshank chaparral and mixed chaparral because the background levels of seeders and resprouters vary between these vegetation types. To meet the assumptions of ANOVA, shrub height and density were natural log transformed.

Results

Identifying Post-Fire Restoration Priorities in the Copper Fire, Angeles National Forest

The pre-fire vegetation of the Copper Fire is dominated by four WHR vegetation types: mixed chaparral, chamise redshank chaparral, coastal scrub, and annual grassland. Note, based on field knowledge, the area classified as coastal scrub was reassigned to mixed chaparral. Other vegetation types present were either too small in area or classified as a non-shrub lifeform and so were omitted from the PReP tool. WHR vegetation types were stratified by aspect and topography into landscape units (Fig. 2, Step 1).

Based on expert input, both “mixed chaparral south-facing slopes summits and ridges” and “mixed chaparral north-facing slopes, valleys, and depressions” were categorized as ≥40% R + FS species. Mixed chaparral in other southern California landscapes might be classified as 10–40% R + FS species, but

the high abundance of the resprouting species Eastwood manzanita (*Arctostaphylos glandulosa*) warranted a higher % R + FS classification. Likewise, both landscape units of chamise red-shank chaparral were categorized as 10–40% R + FS as field knowledge indicated a high proportion of annual grasses. Both “annual grassland” landscape units had <10% R + FS species. Points were assigned accordingly based on the resprouter and facultative seeder proportions (Table S2).

In terms of fire history (Step 2 of the tool), most of the Copper Fire (61%) had experienced one fire in the last 40 years (prior to 2002), but a small portion (1%) had experienced three fires in 40 years, resulting in a 1 point reduction for those pixels (Fig. 2). The majority of the fire (96%) had burned >5 years ago. For the 4% that had burned within 0–5 years (Fig. 2), pixel scores were reduced by 2 points. No modification of pixel scores was made for the Copper Fire based on drought or season of fire (Step 3). The NOAA PDSI indicated that neither the November 2001–May 2002 growing season pre-fire nor the two post-fire years were categorized as severe or extreme drought. In addition, the fire started in the dry season (June), consequently, no modifications were made to pixel scores relating to drought.

The majority of the Copper Fire was above the 0.2 threshold of annual grass cover (indicated by herbaceous cover from Park et al. 2018) (Fig. 2, Step 4). Where pixels were above this threshold and dominated by obligate seeders (10–40% and <10% R + FS), 1 point was subtracted from the pixel score.

After completing Steps 1–4, the tool provided a map of the regeneration capacity of the pre-fire vegetation based on the intrinsic regeneration potential of the species present

(determined by its reproductive strategy) and modified by fire history, drought tolerance pre- and post-fire, and annual grass cover in each pixel (Fig. 3A). There were five levels of regeneration capacity identified (high, moderate-high, moderate, moderate-low, and low). The tool estimated 9% or 665 ha (1,642 acres) had low regeneration capacity and one-fifth or 1,464 ha (3,618 acres) had high regeneration capacity (Fig. 3A). Since the Copper Fire occurred over 18 years ago, the output produced at the end of Step 4 (without integrating soil erosion risk) is the most valuable for informing post-fire restoration and activities (Wohlgemuth et al. 2009).

Finally to demonstrate the inclusion of erosion risk (Step 5), we used data from the Copper Fire BAER assessment, which showed most of the fire had <50 tons/ha of erosion (associated with a one in 5-year erosion event), with 50–100 tons/ha in the northern part (Fig. 2). The final output map from the tool shows the integration of the soil erosion risk data with the other inputs (Fig. 3B). A comparison of the outputs of Steps 4 and 5 (Fig. 3A & 3B) shows that low regeneration capacity areas in the southern portion of the Copper are also areas of high and very high degradation risk. However, integrating data on soil erosion risk highlights additional areas in the north-east, within high natural regeneration areas (Fig. 3A).

Field Validation of Tool Outputs in the Powerhouse Fire, Angeles National Forest

Does the Cover of Grasses and Shrubs Vary by Regeneration Class? We found coarse vegetation types, excluding annual

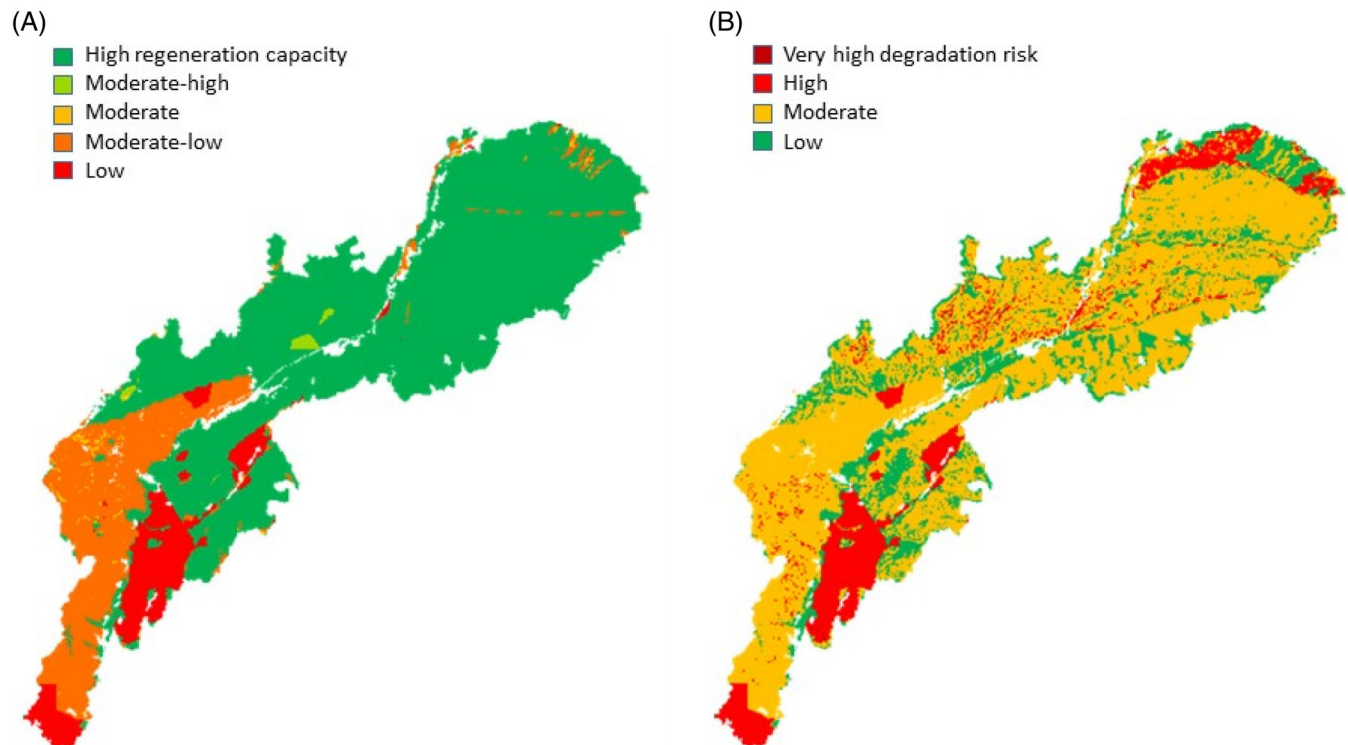


Figure 3. Outputs from the PReP tool for the Copper Fire: (A) regeneration capacity and (B) degradation risk based on the integration of soil erosion data with regeneration capacity (A).

grassland, characterized with low regeneration capacity (low) exhibited higher grass ($F_{3,32} = 6.12, p = 0.002$; Fig. 4A) and herbaceous cover ($F_{3,38} = 4.19, p = 0.012$; Fig. 4B) than those in higher regeneration capacity classes (moderate-low, moderate, high). Grasses covered approximately half of the sampled area ($48\% \pm 3.1$) in the low class, and the non-native annual species *Avena barbata*, *Bromus madritensis*, *Bromus tectorum*, and *Festuca myuros* were the largest contributors to this cover, accounting for 74%. Herbaceous cover was also significantly higher in the low class compared to the other classes, with the non-native annual forbs *Hirschfeldia incana* and *Erodium cicutarium*, and native annual forbs *Eriogonum roseum* and *Deinandra fasciculata* being the most abundant.

Consistent with expectations, native shrub cover was lowest in the low regeneration class and significantly higher in all other classes ($F_{3,47} = 6.76, p < 0.001$; Fig. 4C). When the annual grassland sites were included, the same trend persisted, such that grass cover in the “low” class was significantly higher than all other regeneration capacity classes, including high ($F_{3,37} = 8.27, p < 0.001$). Topographic position (aspect \times topography) had no effect on the cover of grasses ($F_{1,29} = 1.30, p = 0.264$), herbs ($F_{1,35} = 0.003, p = 0.958$), or shrubs ($F_{1,44} = 1.35, p = 0.251$).

Total density of shrubs did not differ among the regeneration classes ($F_{3,47} = 0.30, p = 0.82$), although density per transect (30 m^2) tended to increase from low to high classes (Low:

44.2 ± 11.3 , Moderate-Low: 61.9 ± 9.05 , Moderate: 68.4 ± 11.3 , High: 140 ± 47.0 , mean \pm 1SE).

Does the Proportion of Seeders Versus Resprouters vary by Regeneration Class?. To evaluate whether seeders and resprouters were disproportionately affected by degradation, we evaluated differences in the cover, density, and height of resprouting (R + FS) versus seeding (S) shrubs. In chamise redshank chaparral, cover of resprouters and seeders varied by regeneration class ($F_{2,51} = 4.12, p < 0.05$, Fig. 5A). The relative cover of resprouters was lowest in the low regeneration class compared to moderate-low and moderate classes (Tukey test $p < 0.05$) but cover of seeders did not vary by regeneration class. Moreover, resprouters contributed more cover than seeders in moderate-low and moderate classes (Tukey test $p < 0.05$). In mixed chaparral, the high regeneration capacity class was similar to the chamise redshank chaparral moderate-low and moderate classes, where resprouters exhibited greater cover than seeders ($F_{1,40} = 32.27, p < 0.001$; Fig. 5B).

In chamise redshank chaparral, the density of seeding shrubs was lowest in the low regeneration class ($F_{2,51} = 4.94, p < 0.05$) but also varied by regeneration capacity ($F_{2,51} = 3.61, p < 0.05$), such that the low regeneration class had fewer seeding shrubs (7.67 ± 3.4 per 30 m^2) than the moderate-low

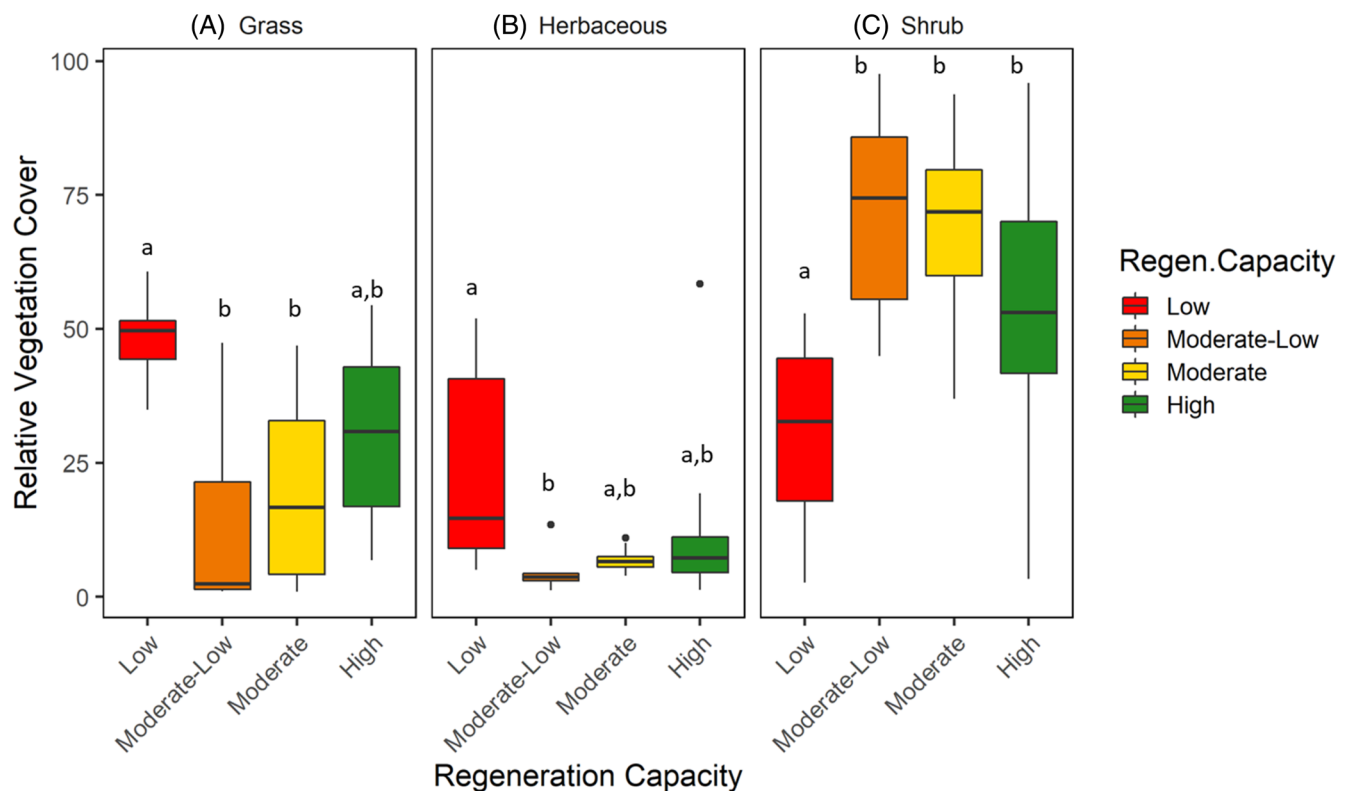


Figure 4. Relative vegetation cover by lifeform from 52 shrubland plots in the Powerhouse Fire, Angeles National Forest. (A) Grass, (B) herbaceous, and (C) shrub cover values across the four regeneration capacity classes. Grass and herbaceous cover include native and non-native species, while shrub cover consists only of native shrubs (given the lack of non-natives at this site). Mixed chaparral and chamise redshank chaparral vegetation types and all landscape positions are pooled together in this analysis. Letters on graphs represent significant differences determined by ANOVA within each lifeform class.

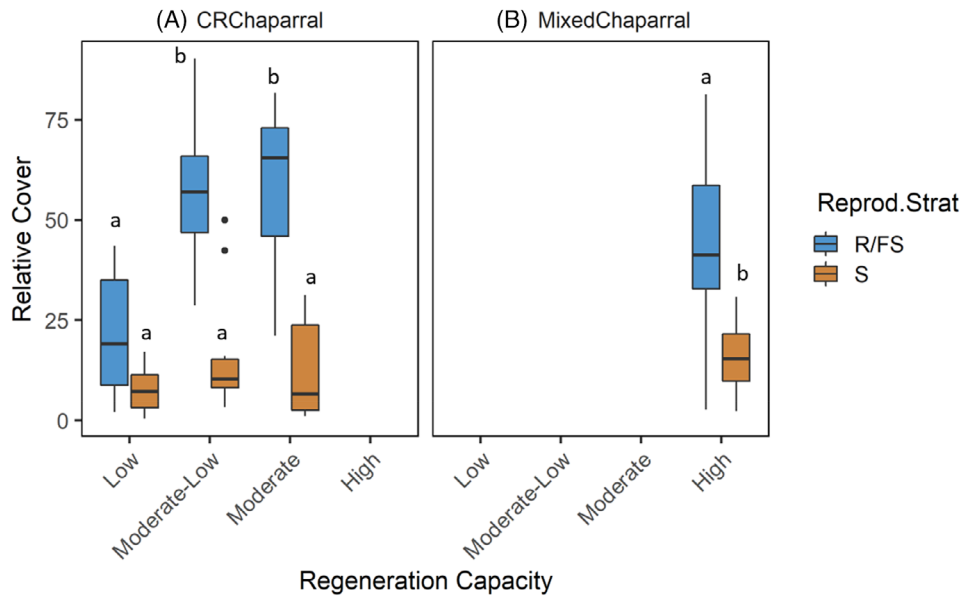


Figure 5. Relative cover of seeder (S) versus resprouter plus facultative seeder (R + FS) species. (A) Chamise redshank chaparral (CRChaparral, 28 plots) and (B) mixed chaparral (28 plots) in the Powerhouse Fire, Angeles National Forest. Letters represent significant differences determined by post-hoc Tukey tests within each vegetation type.

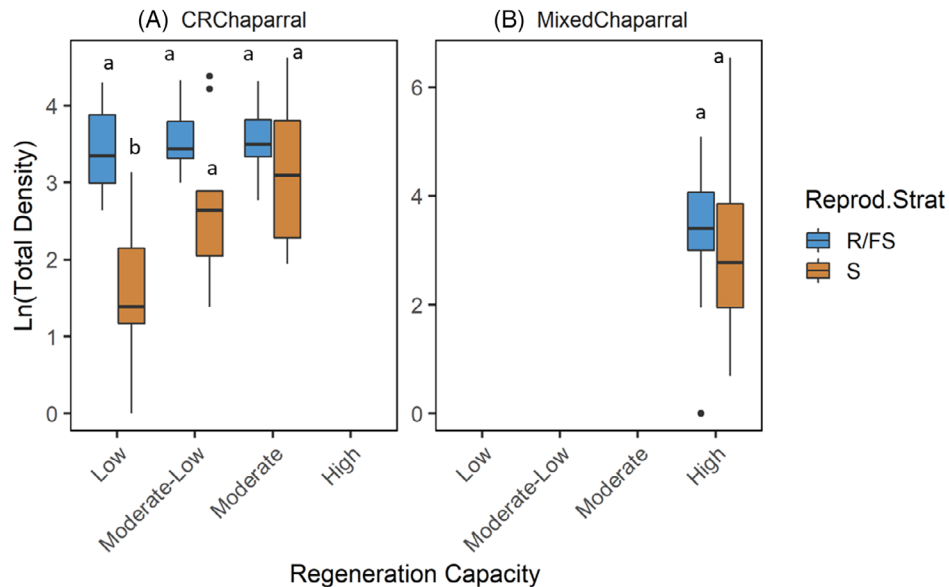


Figure 6. Total density of seeder (S) versus resprouter plus facultative seeder (R + FS) species censused in the 30 m² belt transect. (A) Chamise redshank chaparral (CRChaparral, 29 plots) and mixed chaparral (22 plots) in the Powerhouse Fire, Angeles National Forest. Letters represent significant differences determined by post-hoc Tukey tests within each vegetation type.

(22.82 ± 7.8 per 30 m²) and moderate (33.83 ± 8.9 per 30 m²) classes (Tukey test $p < 0.05$, Fig. 6A). The low regeneration capacity class was dominated by resprouters compared to seeders, and this trend disappeared over the moderate-low and moderate class as the density of seeders gradually increased (Tukey test $p < 0.05$, Fig. 6A). In mixed chaparral, the density of resprouters and seeders were not significantly different ($F_{1,41} = 0.21$, $p = 0.65$; Fig. 6B).

Finally, shrub *height* did not differ by regeneration capacity class for chamise redshank chaparral ($F_{2,51} = 0.27$, $p = 0.77$), although seeders were generally shorter than resprouters ($F_{1,51} = 15.79$, $p < 0.001$). Within the chamise redshank chaparral, there was a significant interaction between regeneration capacity class and regeneration strategy ($F_{2,51} = 4.99$, $p = 0.01$; Fig. 7A). The heights of seeders and resprouters in the low regeneration class were equitable, however, seeding species in the

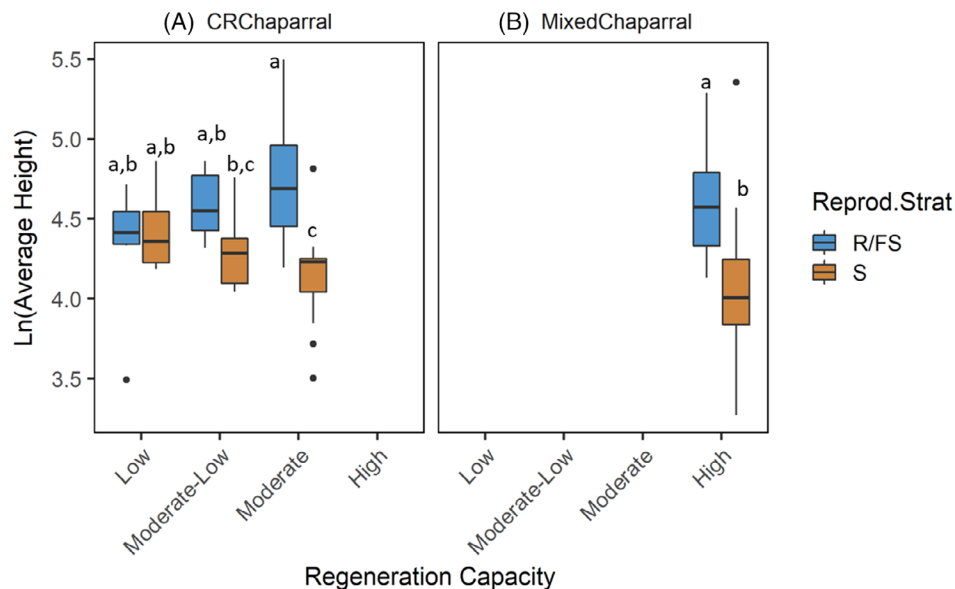


Figure 7. Average height of seeder (S) versus resprouter plus facultative seeder (R + FS) species in chamise redshank chaparral (CRChaparral, 29 plots) and mixed chaparral (22 plots) in the Powerhouse Fire, Angeles National Forest. Letters represent significant differences determined by post-hoc Tukey tests within each vegetation type.

moderate-low and moderate classes were shorter than resprouters. Similarly, resprouters were taller than seeders in the high regeneration class in mixed chaparral ($F_{1,39} = 19.43, p < 0.001$; Fig. 7B).

Discussion

The PReP tool is intended to provide a transparent, simple, and repeatable method for identifying and prioritizing where to allocate limited resources for chaparral shrubland restoration following fire (Safford et al. 2018). While the Powerhouse Fire field monitoring data was not optimal (i.e. not fully factorial) and only represents field validation of one of the two fires we, nonetheless, believe the tool makes a valuable contribution to decision-making by resource managers in shrubland dominated landscapes.

Our assumption that recovery of native shrubland in areas affected by repeat fire and high cover of annual grasses would be impeded, was supported by the field-collected data. Areas in the Powerhouse Fire predicted to have low regeneration capacity exhibited the highest grass (predominantly non-native annual grasses) and herb cover; lowest native shrub cover; and lowest absolute density of shrubs compared to all other regeneration capacity classes. To better understand the drivers of degradation, we examined the cover, density, and height of resprouting (R + FS) and seeding (S) species. A primary assumption of the PReP tool is that obligate seeding species are more sensitive to repeat disturbance, annual grasses, and post-fire drought than resprouting species (Zedler et al. 1983; Pratt et al. 2014; Syphard et al. 2018). Consequently, we assumed seeders would be disproportionately affected compared to resprouters. Field data from the chamise redshank

chaparral vegetation type, showed that not only was shrub cover lower in low regeneration capacity areas, but resprouting species contributed proportionally more than seeding species to shrub cover in moderate-low and moderate classes. Density was also the lowest in the low regeneration class, but differences in reproductive strategies were only present in the low regeneration class. In sum, we observed that the low regeneration class was characterized by low cover of resprouters, and fewer seeding individuals. As the regeneration capacity increased (from low to moderate), we observed an increase in resprouter cover, equitable density of resprouters and seeders, and taller resprouting individuals. Together these findings support the PReP tool outputs for the Powerhouse Fire and provide evidence that native shrub cover, density, and height following fire are significantly modified.

For resource managers faced with huge fire scars, the tool streamlines the daunting task of identifying where within them should be restored. For example, within the 7,300 ha Copper Fire, we identified 665 ha (9%) of the fire scar as candidate areas for restoration and in the Powerhouse Fire 1,532 ha (14%). Output maps from the tool can be downloaded as geotiff rasters and integrated with other spatial data, such as slope steepness or distance from roads or trails, to further refine priority sites into those practical for undertaking restoration. Once the location of restoration has been determined and ground-validated, an appropriate palette of native species can be selected along with best practices for restoring degraded chaparral landscapes (VinZant 2019a, 2019b, Molinari et al. 2021).

The Powerhouse Fire field data provide guidance on which post-fire reproductive strategy could be used in restoration. If the goal of restoration in degraded sites is to promote plant

diversity, then restoration efforts should focus on enhancing species that regenerate from seed since this was the reproductive strategy most affected. Other studies have also shown seeders to be more sensitive to repeat disturbances like fire (Zedler et al. 1983; Haidinger & Keeley 1993). However, if the primary restoration objective is to rapidly reestablish native shrub cover that can reduce the risk of erosion, then using resprouting chaparral species may be more effective, or perhaps sage scrub species with fast growth and maturation. Our field data support this restoration strategy since resprouting species were better able to establish cover and grow more rapidly (height) than seeding species within the first 6 years after the Powerhouse Fire. Moreover, the density and height of resprouting species did not fluctuate strongly with regeneration capacity class, suggesting resprouters are more tolerant of post-fire stressors such as grass competition and multiple fires and may be more likely to persist as these pressures continue in the future.

The shrubland vegetation, fire history, and extent of annual grasslands within the Copper and the Powerhouse fires are characteristic of many of the public lands in southern California region, and so we believe the tool has wide applicability to other areas in southern California as well as to shrublands in general which account for 9% of the natural vegetation in the state of California (Rundel 2018). Some inputs into the tool (fire history, time since last fire, and drought) utilize data updated at least annually and the herbaceous cover data (Park et al. 2018), which indicate annual grass cover, will be potentially updated in the future.

The extent to which restoration post-fire occurs in Mediterranean-type climate regions varies. In Spain, for example, the development of spatial frameworks to identify areas for ecosystem restoration to prevent erosion and protect watersheds is well developed (Duguy et al. 2012; Alloza et al. 2016). In contrast, in South Africa post-fire restoration efforts are triaged based on where to implement soil erosion measures to protect human infrastructure and where to undertake invasive tree control (Holmes et al. 2018; Mostert et al. 2018). However, where restoration post-fire is conducted, we believe the PreP tool could be applied or adapted. At its foundation, the PreP tool requires an understanding of the post-fire life history traits (i.e. responses of resprouting and seeding species) that determine the regeneration success of shrubs. Information and data on life history traits appears well documented in the literature, e.g. Clarke et al. 2015 (Australia); Armesto et al. 1995 (Chile and California); and Gordon & White 1994 (California).

The other key component for implementing the tool relates to the spatial inputs: are the layers used for estimating regeneration success in southern California appropriate for other MTC regions? If so, then data on fire history, non-native species, and pre- and post-fire drought conditions need to be compiled for the new geographic area. Data on drought conditions are likely readily available for all MTC regions (either at regional or national scale), along with fire history, however, data on non-native species might be more challenging to compile. Once compiled, input will be needed from ecologists and resource managers on how to weight the data layers and select decision thresholds based on their relative importance for shrublands in different regions.

In some MTC regions, other factors for guiding restoration decisions might be more important. For example, the successful regeneration of degraded matorral in Chile (whether from fire or other influences) relies heavily on remnant patches of native shrubs to provide propagules for recruitment and low levels of livestock grazing (Holmgren et al. 2000; Armesto et al. 2020). Similarly, in the lowland fynbos in South Africa, high levels of fossorial mammal activity affect the persistence of shrub seed banks compared to mountain fynbos where soil-stored seed banks are more persistent following fire and so resilience is higher (Holmes et al. 2020). If spatial data on these themes are available, the tool's python code could be rewritten to adapt the framework to integrate them.

There are number of examples of spatial tools for prioritizing restoration (in general) from MTC regions. For example, prioritization tools in South Africa are linked to invasive tree removal with the assumption that passive restoration occurs thereafter (Karen Esler, personal communication, 2021). Alternatively, in Australia, the conservation planning tool, Zonation, has been used to determine spatial priorities for revegetation for 62 bird species in cleared agricultural lands (Thomson et al. 2009). This also includes a temporal prioritization which accounts for the time lag between planting and the provision of habitat for birds. Outside of MTC regions, tools such as Restoration Opportunities Assessment Methodology (ROAM) have been developed by the World Resource Institute and the International Union for Conservation of Nature, to give a broad, holistic assessment of restoration opportunities at national and sub-national levels, which involves stocktaking, mapping, restoration costs and benefits analysis, and financing and investment options (Chazdon & Guariguata 2018).

By developing the PreP tool and making it adaptable to other regions with the inclusion of spatial data for a new geographic region or inclusion of new types of data, we hope to increase the tools available for resource managers to restore native shrublands post-fire. Given that 2021 has been hailed as the United Nation's Decade of Ecological Restoration, our work provides a science-based tool for resource managers, widely applicable to shrublands throughout California and potentially to other MTC regions, to identify regeneration capacity on the ground and thus provide a blueprint for shrubland restoration post-fire.

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Supporting Information

The following information may be found in the online version of this article:

Data S1. Setting up the PReP tool.

Table S1. Characteristic native species within the Copper Fire.

Table S2. Assignment of regeneration potential scores based on the relative proportion of resprouting plus facultative seeding post-fire reproductive strategies.

Table S3. Modification of regeneration capacity score based on number of fires in last 40 years in each pixel.

Table S4. Modification of regeneration capacity score based on Time Since Last Fire.

Table S5. Modification of regeneration capacity score in pixels with ≥40% resprouter plus facultative seeders (R+FS), based on occurrence of severe or extreme drought in >four of the seven months of the growing season (November to May) before the fire.

Table S6. Modification of regeneration capacity score in pixels with 10 to 40% and <10% resprouter plus facultative seeders (R+FS), based on occurrence of fire during the wet season.

Table S7. Modification of regeneration capacity score based on whether above or below user-specified threshold of percent cover of annual grasses.

Table S8. Integration matrix for the regeneration capacity (based on post-fire reproductive strategy, fire history, pre- and post-fire drought, and annual grass cover) and BAER erosion risk data to indicate the degradation risk of pixels post-fire.

Figure S1. Modification of regeneration capacity score in pixels.

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