

## RESEARCH ARTICLE

# Prescribed burning may produce refugia for invasive forb, *Oncosiphon pilulifer*

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Prescribed burning is a common management technique to reduce non-native grass cover and seed availability in temperate forests and grasslands; however, its effectiveness in reducing non-native forbs is unclear. Litter of invasive forbs like *Oncosiphon pilulifer* are not consumed by fire like invasive grass litter is, resulting in residual singed stands and high heterogeneity in the postburn landscape. We investigated the potential for this incomplete burning to alter postfire establishment of native and non-native plant species by conducting a field experiment in a prescribed burn in Lake Perris State Park, CA. We investigated the role of microclimate and seed availability on establishment for 2 years following a prescribed burn in both singed stands and completely burned patches by adding or removing litter and adding native seed in a factorial design. Litter presence reduced soil temperatures and light availability, while singed stands had lower soil moisture and temperature. Litter present treatments had  $5.6 \pm 5.9\%$  (mean  $\pm$  SE) greater *Oncosiphon* cover yet doubled *Oncosiphon* viable seeds in the seedbank. Singed stands had  $22.6 \pm 4.9\%$  greater *Oncosiphon* cover and more than doubled *Oncosiphon* viable seeds. Native seed addition did not influence native or *Oncosiphon* cover. These results suggest that residual singed stands within the prescribed burn landscape can create a favorable microclimate and allow *Oncosiphon* to retain seed, increasing reinvasion. Our experiment suggests that litter increased establishment of non-native species as these species may better utilize postburn establishment opportunities impacting overall community recovery. Management of invasive forbs with prescribed burns may require secondary treatments to reduce reinvasion.

**Key words:** grassland management, litter, microclimate, postburn heterogeneity, seed addition, seed availability, seedbank, stinknet

## Implications for Practice

- Postfire heterogeneity from incomplete consumption of invasive forbs during prescribed fire forms refugia that allow satellite subpopulations of invaders to spread within burn areas, via alterations to the microclimate and retention of invader seed.
- Prescribed burning may therefore require secondary management strategies to target invasive forbs as they can form refugia and spread within burn areas due to differences in consumption during prescribed burn events compared to invasive grasses.
- Native seed addition did not significantly influence native or invader cover, suggesting native seed addition alone is insufficient to enhance native cover for postburn restoration efforts.

## Introduction

Prescribed burns are a multifaceted management tool used within many temperate grasslands and forests to mitigate biodiversity loss (Valkó et al. 2014; Valkó & Deák 2021). In North American grasslands and forests, prescribed burning techniques have been used for centuries by traditional practices of indigenous people and are a common modern practice for a variety of goals including the reduction of non-native plant cover and increasing establishment success of native plants (Kimmerer &

Lake 2001). When this tool is applied to invasive forbs, the postburn landscape may not confer these management benefits due to differences in fuel type compared to the invasive grasses that are more commonly the targets of prescribed burning (Pyke et al. 2010; Padullés Cubino et al. 2018); however, there is a substantial research gap investigating the relationships between fire and forb invasion (Tomat-Kelly & Flory 2022). Fire is a heterogeneous disturbance and does not consume fuel evenly across the landscape causing patch-based differences within the burns (Platt & Connell 2003). This heterogeneity can result in refugia for plant species present preburn to spread within the burn area. For invaded landscapes, these refugia might facilitate reestablishment of invaders or promote establishment of different resident non-native species rather than increase establishment of native species (Larios et al. 2013). Increasing the success of prescribed burns thus requires an understanding of the mechanisms

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that mediate postburn establishment within a heterogeneous landscape.

Postburn establishment can be mediated by the stressful environmental situations present postburn such as low water availability and increased temperatures (Iverson & Hutchinson 2002; Kuppinger et al. 2010), yet naturally occurring litter from singed stands might act as microclimate refugia, alleviating these stressful environmental conditions. Dryland restoration has demonstrated that installing shelters or debris can simulate nurse plant effects ameliorating stressful local environmental conditions to promote seedling establishment (Fick et al. 2016). Establishment and early growth are the most sensitive stages of seedling establishment (Grubb 1977; Fenner & Thompson 2005) and singed stands may similarly provide a favorable microclimate reducing mortality during early life stages by functioning like artificial shelters. While native species may benefit from these differences in microclimate and have improved establishment (Okin et al. 2015; Fick et al. 2016), increased competitive interactions from non-native species could impede these outcomes. Non-native species with their fast resource acquisition strategies may more quickly use resources, limiting native performance (Wainwright et al. 2011). Thus, the presence of litter (i.e. singed stands or artificial shelters) postburn can mediate recovery, differentially favoring invasive or native species depending on the interaction of microclimate effects and postburn seed availability.

In postburn settings for annual communities, seed availability is a key driver of system recovery (Connell & Slatyer 1977), and similarly within prescribed burns in annual communities, any residual seed availability will mediate management trajectories to favor species with remnant seeds. Systems with persistent seedbanks that contain native species experience a flush of native establishment after prescribed burns; however, non-native species may reestablish within a few years due to surrounding propagule pressure (Dickens & Allen 2009; Alba et al. 2014). The establishment of non-native species may be accelerated if incomplete consumption results in singed stands of non-native vegetation that still have seeds present either on the plant or in the understory, thus, forming refugia from which a plant invader can spread (Moody & Mack 1988; Weston et al. 2019). These refugia combined with the high seed output of invasive species could therefore result in high cover and reinvasion of treated areas (Fenner & Thompson 2005; Colautti et al. 2006). While prescribed burns are effective at reducing transient invader seedbanks (Reynolds et al. 2001; Keeley et al. 2008), incompletely burned patches that provide refugia for invader seed may thwart achieving management goals such as invader removal and native establishment.

Invader legacies may create additional establishment barriers that prevent the successful establishment of native species in postburn landscapes, necessitating additional management efforts (Larios & Suding 2013). In heavily invaded areas, native seedbanks are often depleted (Cox & Allen 2008; Gioria & Pyšek 2015). Consequently, native seed addition and planting native seedlings are an essential management action for increasing native establishment (Nolan et al. 2021). However, broad-scale seed addition often does not translate to high native establishment, high postemergence seedling mortality results

from environmental conditions and competitive pressures from invasive species (Shackelford et al. 2021). While construction of artificial shelters can help ameliorate stressful conditions (Okin et al. 2015; Fick et al. 2016; Abella & Chiquoine 2019), successful native establishment in these conditions likely needs to be paired with seed addition (Havrilla et al. 2020). Therefore, achieving native management goals postprescribed burn may require selectively adding native seeds to areas with litter.

Such combined management activities are widely used for managing the negative effects of non-native annual grasses in Californian grasslands, which are heavily invaded semiarid ecosystems (Mack 1981; D'Antonio & Vitousek 1992; DiTomaso 2000; Reynolds et al. 2001). However, success of this technique on the small seeded invasive forbs that are increasingly invading these systems is unclear. *Oncosiphon pilulifer*, stinknet, is one such invasive forb that is spreading in southern California grasslands. *Oncosiphon* is emerging as a highly problematic species, as it produces many seeds and can grow under a variety of environmental conditions (Riefner & Boyd 2007). As a new invasive species in North America, management practitioners have less knowledge of the ecology of *Oncosiphon* within the invaded area and limited experience with successful management and eradication efforts. Prescribed burns do not fully consume this invader, leaving behind singed (incompletely burned) stands after burn events, which may facilitate *Oncosiphon* reestablishment, making this a model system to evaluate how postburn heterogeneity may create refugia that mediates postburn recovery.

To address this uncertainty, we asked how do *Oncosiphon* singed stands influence the postburn establishment of native and non-native species? To elucidate the relative contributions of litter and seed availability postburn, we conducted a factorial field experiment to investigate the role of burn completion, litter effects, and native seed addition on postburn community recovery. We hypothesized (1) that postburn litter will function like artificial shelters to alleviate environmental stress resulting in a greater number of species and greater cover within litter treatments postburn and (2) that singed stands will harbor viable seeds from the transient seedbank and provide more favorable microclimates in which *Oncosiphon* can establish postburn, effectively acting as a refugia within burns. Additionally, we hypothesized (3) that native species are seed limited, and the addition of native seeds will increase native cover and establishment will be enhanced by the interaction between the ameliorating effects of litter and seed addition. Despite potential increases in native cover, if these singed stands promote reinvasion, we would predict communities would exhibit a divergent and undesirable trajectory away from native establishment and toward invasive dominance as invaders can outperform and spread faster than natives if native seeds are not present to increase native recruitment.

## Methods

### Study Area and Design

Our study took place in the Lake Perris State Recreation Park (LPSP; 33.87934073, -117.1431129) in Riverside County

California in 2020 and 2021. LPSP experiences a Mediterranean-type climate with warm dry summers, and cooler wet winters. The total precipitation at LPSP during the first year growing season (October through June) was 316 mm, and 125 mm in the second year, and the average temperatures were 15.3°C in the first year and 16.0°C in the second year (PRISM Climate Group 2022). LPSP contains several dominant annual invasive forbs (e.g. *Brassica tournefortii*, *Oncosiphon pilulifer*, *Sisymbrium irio*) and annual grasses (e.g. *Avena fatua*, *Bromus madritensis*, *Schismus barbatus*) as well as annual native forb species (e.g. *Amsinckia intermedia*, *Calandrinia menziesii*, *Lasthenia platyglossa*). *Oncosiphon* is an *Asteraceae* originally from South Africa and was accidentally introduced to LPSP in the 1980s, where it remained at low densities until the last several years. At the time of the study, *Oncosiphon* had become largely dominant across the reserve.

The LPSP prescribed burn practices are intended to remove invasive plants and create a more favorable habitat for the threatened Stephens' kangaroo rat, *Dipodomys stephensi*. Fire return intervals are determined by visual observation of biomass accumulation, to ensure enough fuel is present to carry fire and to maximize efficacy of burns by waiting until visual thresholds of accumulation are surpassed. Fires are performed in the

morning with temperatures below 29.5°C and with winds from the South West with humidity between 20 and 60%. Fires are executed utilizing drip torches from perimeters, and fire flares into the interior of the fire to assist with developing heat. This study was performed in a 0.914 km<sup>2</sup> area previously burned in 2015 and burned again in June 2019. The burn occurred in the morning and lasted between 3 and 4 hours (K. Kietzer 2023, California State Parks, CA, personal communication). We identified either completely bare ground or intact but singed stands of *Oncosiphon* litter and used this distinction to determine if plots were incompletely or completely burned. The cover of *Oncosiphon* singed stands varied across the postburn landscape from 50 to 100% cover, and we aimed to account for this variation by selecting 10 *Oncosiphon* stands within the prescribed burn area with an even number of mid-level cover (50–80%) and high-level cover (80–100%) stands to implement a factorial experiment and monitor plant recovery dynamics (Fig. 1A). Burn completion was determined in August 2019 when live vegetation was minimal.

We set up an experiment to tease apart the role of burn completion (i.e. complete burn or singed stand), litter presence (i.e. litter or no litter), and native seed availability (i.e. seed, unseed) on native and non-native establishment postprescribed burn. We

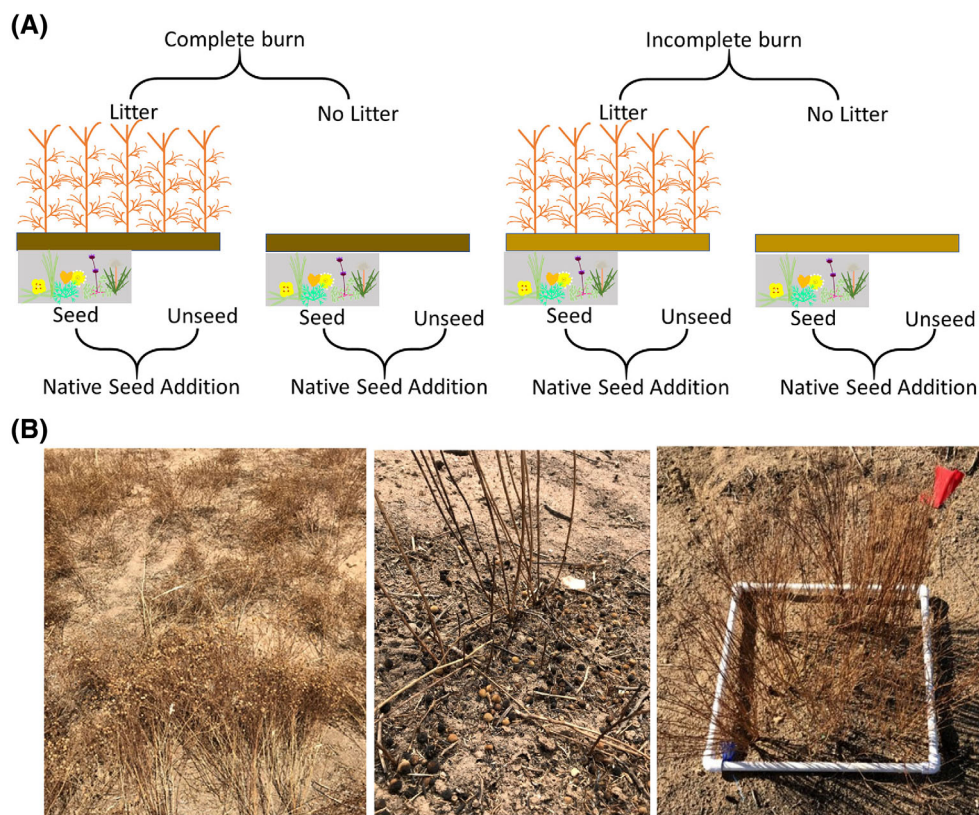


Figure 1. (A) Diagram of experimental groups and (B) images of incompletely consumed *Oncosiphon* singed stands and litter manipulation. (A) Experimental groups include factorial combination of burn completion (complete burn vs. incomplete burn/singed stands), litter treatment (litter vs. no litter), and native seed addition treatments (seed vs. unseeded). (B) The leftmost picture is singed *Oncosiphon* litter, the center picture is of singed inflorescences, and the right image is a litter addition plot. The singed litter were taken from litter removal in singed stands and staked into complete burn + litter plots to create a similar vertical litter structure and total litter cover.



set up four burn and litter treatments: (1) complete burn + no litter, (2) complete burn + litter, (3) singed stand + no litter, and (4) singed stand + litter and crossed these with a native seed addition (i.e. seed or unseed) for a total of eight plots within each of the 10 sites identified above, for a total of 80 plots. The singed stands contained only *Oncosiphon* litter, which retained its vertical structure from the previous year's growth, while more flammable non-native grasses were removed by the fire. We paired litter removal with the litter additions, by taking singed *Oncosiphon* litter from the singed stand + litter removed treatment and staking them in the same arrangement and density in the complete burn + litter treatment (Fig. 1B). We removed any seeds remaining on the litter to isolate litter effects. In the singed stand + no litter, we removed any aboveground singed litter to isolate just the effects of postburn seed availability. The plots were  $0.5 \times 0.5$  m. Each stand of singed *Oncosiphon* formed the basis of a block that was roughly  $15 \text{ m}^2$ . Within these blocks we set up the eight plots so that each complete burn or singed stand plot was placed at least 2 m away from the next treatment plot of complete burn or singed stands, respectively. The complete burn plots were placed at least 5 m away from the edge of *Oncosiphon* stands. Plots were placed haphazardly, where within the singed stand plot locations were focusing on consistency of *Oncosiphon* singed litter cover, and the surrounding complete burn plots were haphazardly placed on bare ground representative of the surrounding complete burn landscape. Our seeding treatment was composed of a diverse mix of dominant and rare native plant species (*Camissoniopsis bistorta*, *Eschscholzia californica*, *Layia platyglossa*, *Salvia columbariae*, *Stipa pulchra*, *Uropappus lindelyi*). All species except for *Stipa pulchra* are annual species that are representative of the dominant ecological strategy in this system. The perennial *Stipa pulchra* was included as it is often included in restoration seed palettes under the assumption that it historically occurred in these areas (Bartolome & Gemmill 1981). The mix was selected in consultation with the LPSP senior environmental scientist and seed was purchased to use locally sourced populations except for *Uropappus lindelyi*, which was collected from a local preserve, Motte Rimrock Reserve, Riverside, CA (33.8005747, -117.2553159). We sowed the native seed mix at a rate of  $8 \text{ g/m}^2$  in November of 2019 before the growing season rains began with each species sowed at  $1.33 \text{ g/m}^2$ .

### Data Collection

We measured plant composition and environmental conditions during peak biomass (April) for 2 years (2020–2021) following the Jepson Flora species names and classifications of origin (Jepson Flora Project 2022). To address the impacts of singed stands on growing conditions, we measured soil volumetric water content (VWC) with a soil moisture probe (Campbell Scientific, Hydrosense II), soil surface temperature with a digital thermometer (Carolina Digital Pocket Thermometer), and light with a photosynthetically active radiation (PAR) meter (AccuPAR LP-80, Meter Group), within a week of plant composition measures (April). For the VWC and soil temperature measures, three points were measured in each plot and

averaged together. To measure PAR, we simultaneously measured PAR above the canopy level and at the ground level between 11:30 and 13:30 hours, to calculate the proportion of light reaching the ground. We replicated our PAR measures twice for each plot, then averaged the proportions to have one measure per plot.

To measure plant community responses, we made visual estimates of species composition, where we recorded percent cover for each vascular plant species within a plot. All layers of the canopy were included in our visual estimates of percent cover, and thus the plot cover totals can be greater than 100%. To identify differences in surface seedbank composition, we additionally performed a 5-month seedbank study from November 2021 to May 2022 in a University of California Riverside greenhouse. In each experimental plot, we scraped the top 250 mL of soil (top 1 cm) from each whole plot in April 2021 as this was the end of the growing season with peak seed production and thus the time to have the most representative seed availability at the end of our experiment. Each soil sample was spread across a  $25 \times 25$ -cm tray and covered with a thin layer of sand. The trays were placed in stratified greenhouse blocks to ensure no replicates from the same field block were included in the same greenhouse block. Ten greenhouse blocks were randomized biweekly to minimize greenhouse effects. All seedlings were identified and removed to prevent double counting or transplanted and then grown to the point of flower to ensure identification. Our *Oncosiphon* focal response variables were percent cover from visual field estimates, as well as total number of viable seeds in our greenhouse seedbank study. To address native species responses, we focused on total native cover, seeded species cover, seeded species richness from the field study, and total native viable seeds for all native plants and seeded species viable seeds from the greenhouse study.

### Analyses

Due to strong differences in precipitation between years that strongly regulated plant performance, we performed separate models for 2020 and 2021. This approach allowed us to decipher the impacts of our experimental treatments without the effect of precipitation overwhelming treatment effects; however, as the data from 2021 is dependent upon treatments imposed in 2020, these data should be interpreted as a continuation of the first analysis rather than independent analyses. To quantify differences in microclimate, we performed a linear mixed effects model on VWC, soil surface temperature, and proportion available light with the fixed effects of burn completion, litter treatment, and seed treatment as well as all interactions, and block with nested factor of initial *Oncosiphon* singed stand density as the random effect.

We performed a linear mixed effects model with the random effect of block with initial *Oncosiphon* singed stand density nested within block, and fixed effects of burn completion, litter treatment, and seed treatment as well as all interactions for *Oncosiphon* field cover, total native cover, seeded species cover, and seeded species richness responses. For viable seed responses, including *Oncosiphon*, total natives, and seeded

natives, we performed a linear mixed effects model with the fixed effects of burn completion, litter treatment, seed treatment, as well as all interactions and greenhouse block and field block as the random effects. While we seeded a total of six species, *Stipa pulchra* had zero percent cover in the field and none germinated in our seedbank study. Due to the substantial number of plots with no seeded species we utilized a linear mixed effects model on  $\ln(x + 1)$  transformed data for seeded species cover and total number of seeded species present.

To address community level responses, we focused on univariate and multivariate responses. We calculated Shannon–Weiner diversity ( $H$ ) using the “vegan” package (v.2.6-2; Oksanen et al. 2022), and calculated species richness as the sum of all species within a plot. For both  $H$  and richness, we performed a linear mixed effects model with the fixed effects of burn completion, litter treatment, and seed treatment as well as all interactions and block with nested factor of initial *Oncosiphon* singed stand density as the random effect. To address how burn completion, litter and seed treatments influence overall community composition over time, we performed a PERMANOVA with the fixed effects of burn completion, litter treatment, and seed treatment and all interactions and block with nested factor of initial *Oncosiphon* singed stand density as a random effect and the response variable was the matrix of cover for each species present in a plot. Statistically significant differences between factors from the PERMANOVA are visualized with a principal coordinates analysis (PCoA).

All analyses were performed in R (v.4.0.2). All linear mixed effects models were performed using the “lme4” package (Bates et al. 2015). Post hoc tests were performed using the emmeans function in the “emmeans” package (Russell 2022). PcoA was performed using the “mass” package (Venables & Ripley 2002) and PERMANOVA was performed using the adonis function in the “vegan” package (v.2.6-2; Oksanen et al. 2022). Data were transformed as needed to achieve normality in model residual distributions, where soil moisture, *Oncosiphon* cover, total native cover, total seeded cover, *Oncosiphon* viable seeds, total native viable seeds, and total seeded species viable seeds were  $\ln(x + 1)$  transformed and PAR was cube transformed.

## Results

Over our 2-year study, we observed 27 vascular plant species in our field plots—13 non-native and 14 native species (Table S1). Native cover ranged from 0 to 53% with an average of  $7.3 \pm 0.8\%$  SE, and non-native cover ranged from 5 to 102.5% with an average of  $60.2 \pm 1.9\%$  SE cover in both years combined. Within our seedbank study we found 32 species, 14 non-native species and 18 native species (Table S2). The total native viable seeds—pooled for all species—ranged from 2 to 515 with an average of  $92.5 \pm 9.8$  SE, and total non-native viable seeds ranged from 9 to 498 with an average of  $133.1 \pm 10.7$  SE.

**Table 1.** Summary statistics for environmental metrics. The first number is the  $F$  statistic, the following numbers in subscript are Satterthwaite approximations of the degrees of freedom with numerator and denominator separated by a comma, with  $p$  values afterwards. Soil moisture was measured by volumetric water content, and  $\ln(x + 1)$  transformed, soil surface temperature was not transformed, and percent available PAR was cube transformed.

	2020 $F$ Stat <sub>df</sub> ; $p$ Value	2021 $F$ Stat <sub>df</sub> ; $p$ Value
Soil moisture		
Burn completion	37.99 <sub>[1,61.217]</sub> ; <0.0001	9.46 <sub>[1,63.127]</sub> ; 0.003
Litter treatment	0.12 <sub>[1,61.217]</sub> ; 0.735	0.11 <sub>[1,63.127]</sub> ; 0.743
Seed treatment	0.04 <sub>[1,61.217]</sub> ; 0.847	0.29 <sub>[1,63.127]</sub> ; 0.592
Burn $\times$ litter	0.01 <sub>[1,61.217]</sub> ; 0.932	0.17 <sub>[1,63.127]</sub> ; 0.680
Burn $\times$ seed	0.69 <sub>[1,61.217]</sub> ; 0.409	2.35 <sub>[1,63.127]</sub> ; 0.130
Litter $\times$ seed	0.54 <sub>[1,61.217]</sub> ; 0.466	0.91 <sub>[1,63.127]</sub> ; 0.343
Burn $\times$ litter $\times$ seed	0.12 <sub>[1,61.217]</sub> ; 0.726	0.63 <sub>[1,63.127]</sub> ; 0.431
Soil surface temperature		
Burn completion	25.93 <sub>[1,62.787]</sub> ; <0.0001	21.27 <sub>[1,63.305]</sub> ; <0.0001
Litter treatment	27.18 <sub>[1,62.787]</sub> ; <0.0001	19.34 <sub>[1,63.305]</sub> ; <0.0001
Seed treatment	0.09 <sub>[1,62.787]</sub> ; 0.771	0.28 <sub>[1,63.305]</sub> ; 0.599
Burn $\times$ litter	1.40 <sub>[1,62.787]</sub> ; 0.241	0.34 <sub>[1,63.305]</sub> ; 0.562
Burn $\times$ seed	0.53 <sub>[1,62.787]</sub> ; 0.469	0.47 <sub>[1,63.305]</sub> ; 0.497
Litter $\times$ seed	2.63 <sub>[1,62.787]</sub> ; 0.110	0.36 <sub>[1,63.305]</sub> ; 0.552
Burn $\times$ litter $\times$ seed	1.46 <sub>[1,62.787]</sub> ; 0.232	1.39 <sub>[1,63.305]</sub> ; 0.243
Percent available PAR		
Burn completion	0.30 <sub>[1,59.361]</sub> ; 0.588	3.25 <sub>[1,62.278]</sub> ; 0.076
Litter treatment	88.74 <sub>[1,59.361]</sub> ; <0.0001	19.18 <sub>[1,62.278]</sub> ; <0.0001
Seed treatment	1.27 <sub>[1,59.361]</sub> ; 0.264	0.53 <sub>[1,62.278]</sub> ; 0.468
Burn $\times$ litter	0.25 <sub>[1,59.361]</sub> ; 0.621	3.81 <sub>[1,62.278]</sub> ; 0.055
Burn $\times$ seed	0.05 <sub>[1,59.361]</sub> ; 0.825	0.87 <sub>[1,62.278]</sub> ; 0.355
Litter $\times$ seed	0.18 <sub>[1,59.361]</sub> ; 0.677	0.11 <sub>[1,62.278]</sub> ; 0.739
Burn $\times$ litter $\times$ seed	0.02 <sub>[1,59.361]</sub> ; 0.901	0.05 <sub>[1,62.278]</sub> ; 0.828

### Microclimate Response

The microclimate was significantly different in key aspects among treatment groups in both years. The singed stands had lower VWC than complete burn, and had lower soil temperature (Table 1; Fig. 2A & 2C). Singed stands did not have different amounts of light reaching the ground in 2020 but had less light reaching the ground in 2021 (Table 1; Fig. 2E). Litter presence did not influence soil moisture in either year (Table 1; Fig. 2B); however, the litter treatment was cooler at the surface and had less light reaching the ground (Table 1; Fig. 2D & 2F). Our seeding treatment did not influence soil moisture, soil surface temperature, or the proportion of light reaching the ground (Table 1).

### Oncosiphon Response

The percent *Oncosiphon* cover was significantly higher in the incomplete burn (Table 2; Fig. 3A) where singed stands had  $36.8 \pm 7.66\%$  SE greater *Oncosiphon* cover than the complete burn in the first year, and  $8.33 \pm 4.15\%$  SE greater cover in 2021. The litter treatment in 2020 had  $11.4 \pm 10.0\%$  SE greater *Oncosiphon* cover; however, litter presence did not significantly influence *Oncosiphon* cover in 2021 (Table 2; Fig. 3B). There was consistently greater *Oncosiphon* cover within singed stands; however, there was an interaction between burn completion and litter treatment in 2020 where in the complete burn with litter present, *Oncosiphon* cover increased  $11.88 \pm 4.81\%$  SE

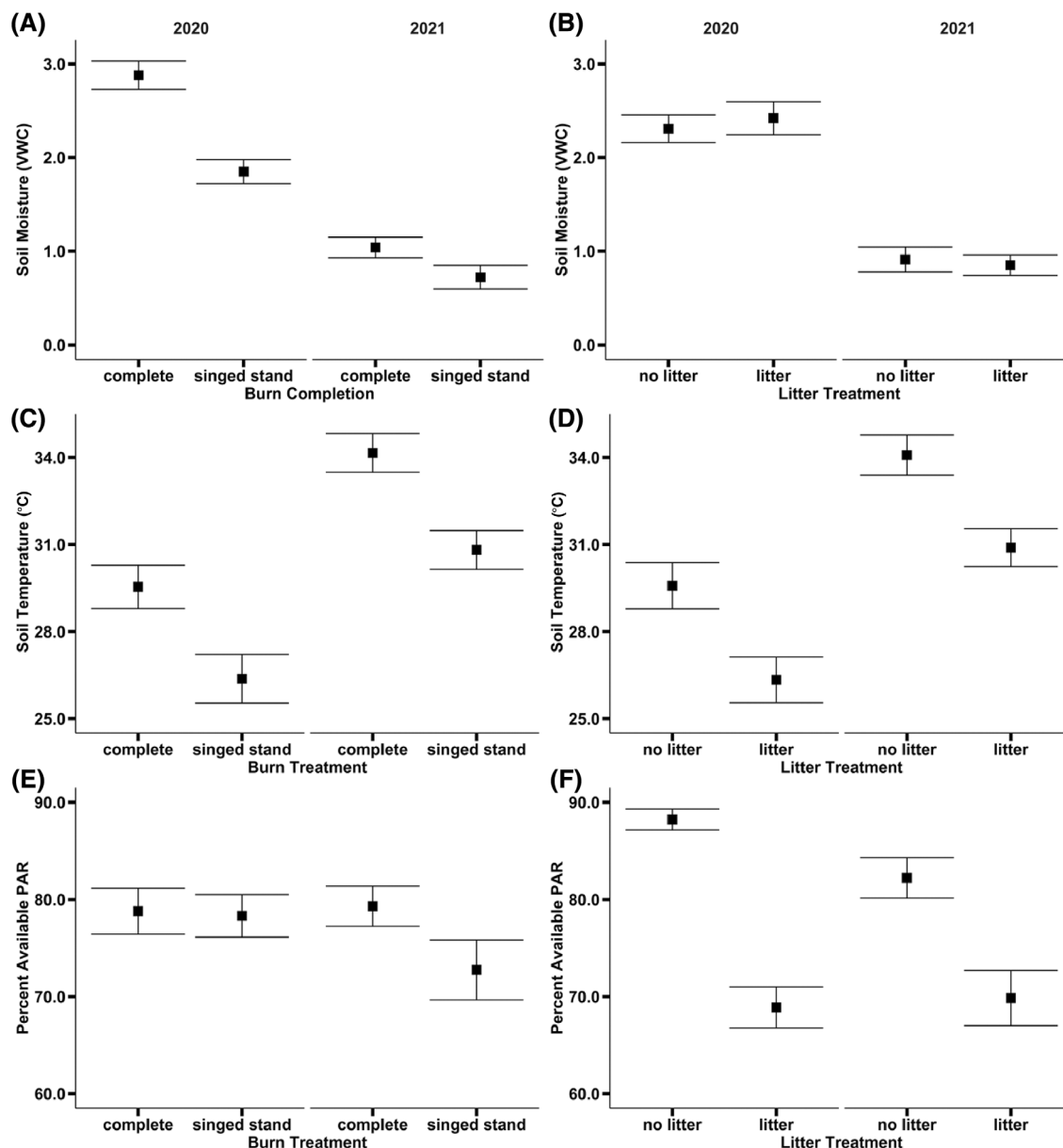


Figure 2. Environmental differences between burn completion treatments (A, C, E) and litter treatments (B, D, F). Averages of soil moisture (A, B), soil temperature (C, D), and percent of available photosynthetically active radiation (E, F). The first year of data collection in 2020 is on the left half of each graph, and the second year in 2021 is on the right half of each graph. Vertical bars represent  $\pm$  SE.

**Table 2.** Summary statistics of *Oncosiphon* responses. The first number is the *F* statistic, the following numbers in subscript are Satterthwaite approximations of the degrees of freedom with numerator and denominator separated by a comma, and the final number is the *p* value. Field response of total *Oncosiphon* cover in 2020 and 2021, and viable seed counts were all  $\ln(x + 1)$  transformed. \*Viable seed was estimated from a seedbank study of soil collected once in 2021.

	Oncosiphon Cover 2020 <i>F Stat</i> <sub>(df)</sub> ; <i>p Value</i>	Oncosiphon Cover 2021 <i>F Stat</i> <sub>(df)</sub> ; <i>p Value</i>	Viable Seed 2021* <i>F Stat</i> <sub>(df)</sub> ; <i>p Value</i>
Burn completion	63.01 <sub>[1,63]</sub> ; <0.0001	22.14 <sub>[1,63]</sub> ; <0.0001	50.51 <sub>[1,55.093]</sub> ; <0.0001
Litter treatment	12.97 <sub>[1,63]</sub> ; 0.001	0.09 <sub>[1,63]</sub> ; 0.768	21.10 <sub>[1,55.093]</sub> ; <0.0001
Seed treatment	0.02 <sub>[1,63]</sub> ; 0.898	0.19 <sub>[1,63]</sub> ; 0.668	0.01 <sub>[1,55.093]</sub> ; 0.920
Burn × litter	4.66 <sub>[1,63]</sub> ; 0.035	0.61 <sub>[1,63]</sub> ; 0.437	6.30 <sub>[1,55.093]</sub> ; 0.015
Burn × seed	0.61 <sub>[1,63]</sub> ; 0.438	0.01 <sub>[1,63]</sub> ; 0.930	0.18 <sub>[1,55.093]</sub> ; 0.672
Litter × seed	0.09 <sub>[1,63]</sub> ; 0.763	2.23 <sub>[1,63]</sub> ; 0.140	0.11 <sub>[1,55.093]</sub> ; 0.745
Burn × litter × seed	0.02 <sub>[1,63]</sub> ; 0.885	0.30 <sub>[1,63]</sub> ; 0.585	2.12 <sub>[1,55.093]</sub> ; 0.151

compared to no litter (Table 2). The interaction between burn completion and litter was not significant in 2021 (Table 2). The addition of native seeds did not have an observed impact on *Oncosiphon* cover (Table 2).

There were more viable *Oncosiphon* seeds in the soil from the singed stands, and with litter present (Table 2; Fig. 3C). Singed stands had more than double the amount of viable *Oncosiphon* seeds with  $123 \pm 15$  SE viable seeds versus  $47 \pm 8$  SE in the complete burn. The litter present plots had  $102 \pm 12$  SE viable seeds compared to  $68 \pm 15$  SE in the no litter plots. The difference between litter treatments was

greatest in the complete burn, where litter in complete burn had  $71 \pm 14$  SE viable seeds compared to  $23 \pm 7$  SE viable seeds in the no litter complete burn (Table 2; Fig. 3C).

### Native Species Responses

Total native cover was higher in complete burn than singed stands in 2020, but not 2021 (Table 3). Total native cover was not influenced by litter treatment or seed addition (Table 3). Our native seed addition increased the total cover, and number of seeded species established in plots in both 2020 and 2021

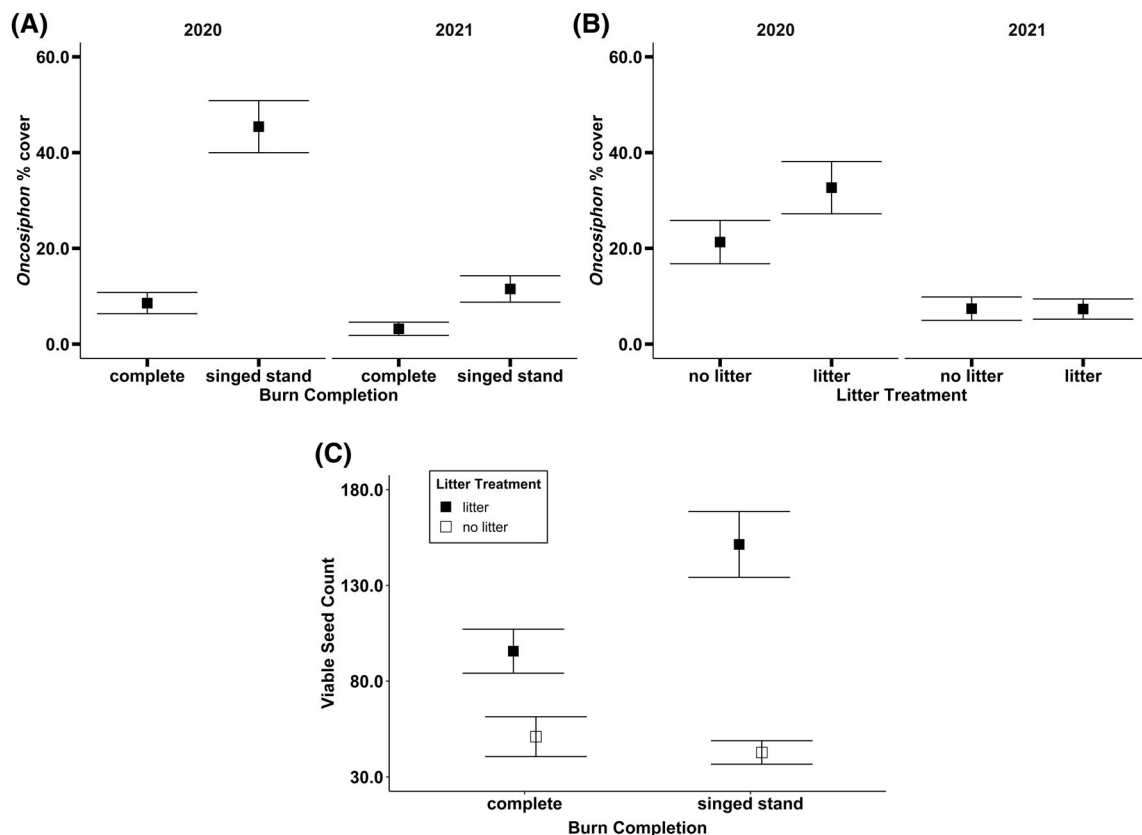


Figure 3. The effect of burn completion (A) and litter treatment (B) on *Oncosiphon pilulifer* percent cover in two consecutive years in the field and on their viable seeds (C), counted during a seedbank experiment in 2021. Analyses were performed using  $\ln(x + 1)$  transformed data, and graphed data display averages of raw data and vertical bars represent  $\pm$  SE.

**Table 3.** Summary statistics of California native species responses. The first number is the  $F$  statistic, the following numbers in subscript are Satterthwaite approximations of the degrees of freedom with numerator and denominator separated by a comma, and the final number is the  $p$  value. Results from the first year are on the left, and results from the second year are on the right. Total native cover, seeded species cover, and seeded species richness were all  $\ln(x + 1)$  transformed.

	2020 $F$ Stat <sub>(df)</sub> ; $p$ Value	2021 $F$ Stat <sub>(df)</sub> ; $p$ Value
Total native cover		
Burn completion	28.86 <sub>[1,63,239]</sub> ; <0.0001	1.31 <sub>[1,72]</sub> ; 0.256
Litter treatment	1.57 <sub>[1,63,239]</sub> ; 0.215	3.89 <sub>[1,72]</sub> ; 0.052
Seed treatment	2.08 <sub>[1,63,29]</sub> ; 0.155	0.72 <sub>[1,72]</sub> ; 0.400
Burn $\times$ litter	3.39 <sub>[1,63,29]</sub> ; 0.070	1.47 <sub>[1,72]</sub> ; 0.229
Burn $\times$ seed	0.07 <sub>[1,63,239]</sub> ; 0.798	0.17 <sub>[1,72]</sub> ; 0.681
Litter $\times$ seed	3.53 <sub>[1,63,239]</sub> ; 0.065	1.28 <sub>[1,72]</sub> ; 0.262
Burn $\times$ litter $\times$ seed	0.06 <sub>[1,63,29]</sub> ; 0.810	0.04 <sub>[1,72]</sub> ; 0.848
Seeded species cover		
Burn completion	2.78 <sub>[1,63]</sub> ; 0.100	0.34 <sub>[1,72]</sub> ; 0.564
Litter treatment	1.36 <sub>[1,63]</sub> ; 0.249	0.43 <sub>[1,72]</sub> ; 0.515
Seed treatment	17.57 <sub>[1,63]</sub> ; <0.0001	53.94 <sub>[1,72]</sub> ; <0.0001
Burn $\times$ litter	0.03 <sub>[1,63]</sub> ; 0.874	2.56 <sub>[1,72]</sub> ; 0.114
Burn $\times$ seed	3.95 <sub>[1,63]</sub> ; 0.051	0.02 <sub>[1,72]</sub> ; 0.886
Litter $\times$ seed	0.71 <sub>[1,63]</sub> ; 0.401	0.05 <sub>[1,72]</sub> ; 0.828
Burn $\times$ litter $\times$ seed	0.44 <sub>[1,63]</sub> ; 0.508	1.36 <sub>[1,72]</sub> ; 0.248
Seeded species richness		
Burn completion	1.56 <sub>[1,63]</sub> ; 0.216	0.00 <sub>[1,72]</sub> ; 1.000
Litter treatment	0.06 <sub>[1,63]</sub> ; 0.803	0.17 <sub>[1,72]</sub> ; 0.677
Seed treatment	22.58 <sub>[1,63]</sub> ; <0.0001	50.50 <sub>[1,72]</sub> ; <0.0001
Burn $\times$ litter	0.06 <sub>[1,63]</sub> ; 0.803	1.57 <sub>[1,72]</sub> ; 0.214
Burn $\times$ seed	1.56 <sub>[1,63]</sub> ; 0.216	0.17 <sub>[1,72]</sub> ; 0.677
Litter $\times$ seed	0.06 <sub>[1,63]</sub> ; 0.803	0.00 <sub>[1,72]</sub> ; 1.000
Burn $\times$ litter $\times$ seed	0.56 <sub>[1,63]</sub> ; 0.456	0.70 <sub>[1,72]</sub> ; 0.406

(Table 3; Fig. S1). The percent cover remained low across all species, with the greatest cover in any plot of all seeded species being 5% in 2020 and 2021 with only a maximum of two seeded species establishing in the same plot in both years. Seeded species cover and species richness of the seeded subset were similar between burn treatment and litter treatment in both years (Table 3). Individually, our seeded species were consistently low in cover, where the highest cover of an individual species was *Layia platyglossa* with an average of  $0.51 \pm 0.16\%$  SE in the seeded plots in 2020, and  $0.40 \pm 0.10\%$  SE in 2021, and

$0.13 \pm 0.13\%$  SE in the unseeded plots in 2020 and 0% in the unseeded 2021 plots. Overall, establishment of seeded native species ranged from 0 to 0.45% cover in the seeded treatment, and species averaged between 0 and 0.02% cover in the unseeded treatment (Table S3).

A greater number of native seeds germinated in our seedbank study in the complete burn with an average of  $105 \pm 16$  SE total native seeds compared to  $75 \pm 10$  SE total native seeds in the singed stands (Table 4). The litter treatment and seed treatments did not influence the number of native seeds that germinated (Table 4). The number of viable seeds of our seeded species present in our greenhouse was consistently low with a range from 0 to 15 individuals. There were no differences in how many seeded species germinated in complete burn ( $3.05 \pm 0.39$  SE) and singed stands ( $3.95 \pm 1.02$  SE) (Table 4). More seeded species were present in the seed treatment (Table 4), with an average of  $4.1 \pm 0.6$  SE seeded species present in seed treatment and  $0.7 \pm 0.11$  SE present in unseeded plots. Within the seeded treatment, there were more seeded species present with litter than with no litter (Table 4).

**Table 4.** Summary statistics of viable seed responses for all native species and the seed addition species. The first number is the  $F$  statistic, the following numbers in subscript are Satterthwaite approximations of the degrees of freedom with numerator and denominator separated by a comma, and the final number is the  $p$  value. Total native viable seeds and seeded species viable seeds were both  $\ln(x + 1)$  transformed for residual normality.

	Total Native Viable Seeds $F$ Stat <sub>(df)</sub> ; $p$ Value	Seeded Species Viable Seeds $F$ Stat <sub>(df)</sub> ; $p$ Value
Burn completion	8.18 <sub>[1,63]</sub> ; 0.006	0.88 <sub>[1,63,504]</sub> ; 0.352
Litter treatment	0.33 <sub>[1,63]</sub> ; 0.570	6.35 <sub>[1,63,504]</sub> ; 0.014
Seed treatment	2.70 <sub>[1,63]</sub> ; 0.105	44.83 <sub>[1,63,504]</sub> ; <0.0001
Burn $\times$ litter	0.12 <sub>[1,63]</sub> ; 0.732	1.47 <sub>[1,63,504]</sub> ; 0.231
Burn $\times$ seed	1.65 <sub>[1,63]</sub> ; 0.204	0.84 <sub>[1,63,504]</sub> ; 0.363
Litter $\times$ seed	0.15 <sub>[1,63]</sub> ; 0.704	7.37 <sub>[1,63,504]</sub> ; 0.009
Burn $\times$ litter $\times$ seed	1.43 <sub>[1,63]</sub> ; 0.236	1.41 <sub>[1,63,504]</sub> ; 0.239

### Community Response

We did not observe a change in diversity ( $H$ ) between singed stands and complete burn in 2020 ( $0.74 \pm 0.05$  SE vs.  $0.78 \pm 0.06$  SE; Table 5) but singed stands had greater diversity in 2021 ( $0.80 \pm 0.06$  SE vs.  $0.55 \pm 0.05$  SE; Table 5). Litter



**Table 5.** Summary statistics of community level responses. For diversity and richness, the first number is the *F* statistic, the following numbers in subscript are Satterthwaite approximations of the degrees of freedom with numerator and denominator separated by a comma, and the final number is the *p* value. For the PERMANOVA, the first number is the *F* statistic and the following number in subscript is the *R*<sup>2</sup>, and the final number is the *p* value.

	2020 F Stat <sub>[df]</sub> ; p Value	2021 F Stat <sub>[df]</sub> ; p Value
<b>Diversity (<i>H</i>)</b>		
Burn completion	0.26 <sub>[1,72]</sub> ; 0.611	10.11 <sub>[1,63]</sub> ; 0.002
Litter treatment	1.61 <sub>[1,72]</sub> ; 0.208	1.15 <sub>[1,63]</sub> ; 0.287
Seed treatment	0.14 <sub>[1,72]</sub> ; 0.710	0.44 <sub>[1,63]</sub> ; 0.508
Burn × litter	2.49 <sub>[1,72]</sub> ; 0.119	0.72 <sub>[1,63]</sub> ; 0.398
Burn × seed	0.18 <sub>[1,72]</sub> ; 0.669	0.00 <sub>[1,63]</sub> ; 0.976
Litter × seed	0.08 <sub>[1,72]</sub> ; 0.777	1.01 <sub>[1,63]</sub> ; 0.320
Burn × litter × seed	0.12 <sub>[1,72]</sub> ; 0.728	0.00 <sub>[1,63]</sub> ; 0.995
<b>Richness</b>		
Burn completion	0.31 <sub>[1,72]</sub> ; 0.581	7.84 <sub>[1,63]</sub> ; 0.007
Litter treatment	0.69 <sub>[1,72]</sub> ; 0.408	0.09 <sub>[1,63]</sub> ; 0.769
Seed treatment	5.56 <sub>[1,72]</sub> ; 0.021	6.27 <sub>[1,63]</sub> ; 0.015
Burn × litter	0.69 <sub>[1,72]</sub> ; 0.408	7.03 <sub>[1,63]</sub> ; 0.010
Burn × seed	0.94 <sub>[1,72]</sub> ; 0.335	0.54 <sub>[1,63]</sub> ; 0.464
Litter × seed	1.56 <sub>[1,72]</sub> ; 0.216	0.00 <sub>[1,63]</sub> ; 1.000
Burn × litter × seed	0.48 <sub>[1,72]</sub> ; 0.490	0.00 <sub>[1,63]</sub> ; 1.000
	F Stat <sub>[R<sup>2</sup>]</sub> ; p Value	F Stat <sub>[R<sup>2</sup>]</sub> ; p Value
<b>PERMANOVA results</b>		
Burn completion	33.59 <sub>[0.302]</sub> ; 0.001	15.36 <sub>[0.161]</sub> ; 0.001
Litter treatment	2.51 <sub>[0.023]</sub> ; 0.050	2.21 <sub>[0.023]</sub> ; 0.048
Seed treatment	0.23 <sub>[0.002]</sub> ; 0.826	2.59 <sub>[0.027]</sub> ; 0.032
Burn × litter	2.08 <sub>[0.019]</sub> ; 0.084	1.26 <sub>[0.013]</sub> ; 0.208
Burn × seed	0.43 <sub>[0.004]</sub> ; 0.572	−0.06 <sub>[−0.001]</sub> ; 0.993
Litter × seed	0.09 <sub>[0.001]</sub> ; 0.943	1.06 <sub>[0.011]</sub> ; 0.259
Burn × litter × seed	0.24 <sub>[0.002]</sub> ; 0.783	0.96 <sub>[0.010]</sub> ; 0.303

treatment did not influence diversity in 2020 (litter:  $0.81 \pm 0.06$  SE vs. no litter:  $0.70 \pm 0.05$  SE; Table 5) or 2021 (litter:  $0.72 \pm 0.06$  SE vs. no litter:  $0.64 \pm 0.06$  SE; Table 5). The seed addition did not statistically influence diversity in 2020 (seed:  $0.77 \pm 0.06$  SE vs. unseed:  $0.74 \pm 0.06$  SE; Table 3) or 2021 (seed:  $0.65 \pm 0.06$  SE vs. unseed:  $0.70 \pm 0.06$  SE; Table 5).

Singed stands had statistically similar species richness in 2020 (complete:  $5.35 \pm 0.29$  SE vs. singed stand:  $5.55 \pm 0.24$  SE; Table 5) but had greater richness in 2021 (complete:  $4.35 \pm 0.25$  SE vs. singed stand:  $5.30 \pm 0.2$  SE; Table 5). The litter treatment did not statistically influence species richness in 2020 (litter:  $5.3 \pm 0.26$  SE vs. no litter:  $0.56 \pm 0.27$  SE) or 2021 (litter:  $4.9 \pm 0.24$  SE vs. no litter:  $4.8 \pm 0.29$  SE; Table 5); however, within the no litter treatment the complete burn area had lower species richness ( $3.85 \pm 0.30$  SE) compared to the singed stands with no litter ( $5.7 \pm 0.41$  SE) (Table 5). The plots with native seed addition had greater species richness in both years (2020 seed:  $5.9 \pm 0.27$  SE vs. unseed:  $5.0 \pm 0.24$  SE; 2021 seed:  $5.3 \pm 0.27$  SE vs. unseed:  $4.4 \pm 0.2$  SE; Table 5).

For our whole community level analysis, the PcoA loadings indicate three main species driving differences in community

types: *Erodium cicutarium*, *Oncosiphon pilulifer*, and *Bromus madritensis*, which are all non-native (Fig. 4). The direction of loadings shifts between years, but *Oncosiphon* remained ordinal to *Erodium* in both years and the singed stand dynamics had similar trends. Burn completion significantly influenced community composition in both years (Table 5; Fig. 4A & 4B). The completely burned plots were mostly dominated by *Erodium* regardless of year, and the singed stand plots were associated with more *Oncosiphon* in 2020 or was split dominated by *Oncosiphon* or *Bromus* in 2021 (Fig. 4A & 4B). Litter also influenced community composition in both years (Table 5), where litter plots were slightly more dominated by *Bromus* and *Oncosiphon* than *Erodium* in 2020 (Fig. 4C) and were split between *Bromus*, *Oncosiphon*, and three other species in 2021 (Fig. 4D). The addition of native seeds did not influence community composition in 2020 but seed addition did statistically influence community composition in 2021, where seeded plots were more dominated by *Erodium* than unseeded plots which were split between *Bromus*, *Oncosiphon*, and three other species (Table 5; Fig. S2), notably none of the seed addition species were significant vectors of plant dominance in the ordination.

## Discussion

Our study demonstrates that postburn heterogeneity in the form of singed forb stands impacts both invader and native establishment, with stronger benefits for the invader thus increasing the risk of reinvasion. The focal invader *Oncosiphon* had greater percent cover and a greater amount of viable seeds in the seed-bank when litter was present, likely a result of the more favorable microclimate created by litter. Additionally, there was greater *Oncosiphon* cover within singed stands (i.e. incomplete burn) in both years and double the amount of viable seeds in singed stands, implying that singed stands were contributing to the retention of *Oncosiphon* seeds postburn. The addition of native seeds did not influence native cover, indicating that additional barriers limit the establishment of native species, beyond seed availability. At a community level, we found three main dominant invasive species: *Erodium cicutarium* (forb), *Bromus madritensis* (grass), and *Oncosiphon pilulifer* (forb) structured postmanagement trajectories. The presence of litter altered the composition of the community to favor *Bromus* and *Oncosiphon*, suggesting that these two invasives are the most successful at taking advantage of ameliorated microclimates postburn. The complete burn area was dominated by *Erodium*, while singed stands were either dominated by *Bromus* or *Oncosiphon*, suggesting a difference in invader seed availability results in two trajectories based on burn completion. These results support the hypotheses that heterogeneity in the postburn landscape can alter establishment via litter-microclimate effects and seed availability and can drive recovery trajectories toward reinvasion.

The postburn landscape is heterogeneous, and differences in microclimate can facilitate invasive establishment postburn. Our findings suggest that litter (whether naturally remaining in singed stands or additions) may act like shelters to form islands of greater establishment for invasive species in arid systems via nurse plant effects (Fick et al. 2016; Abella & Chiquoine 2019).

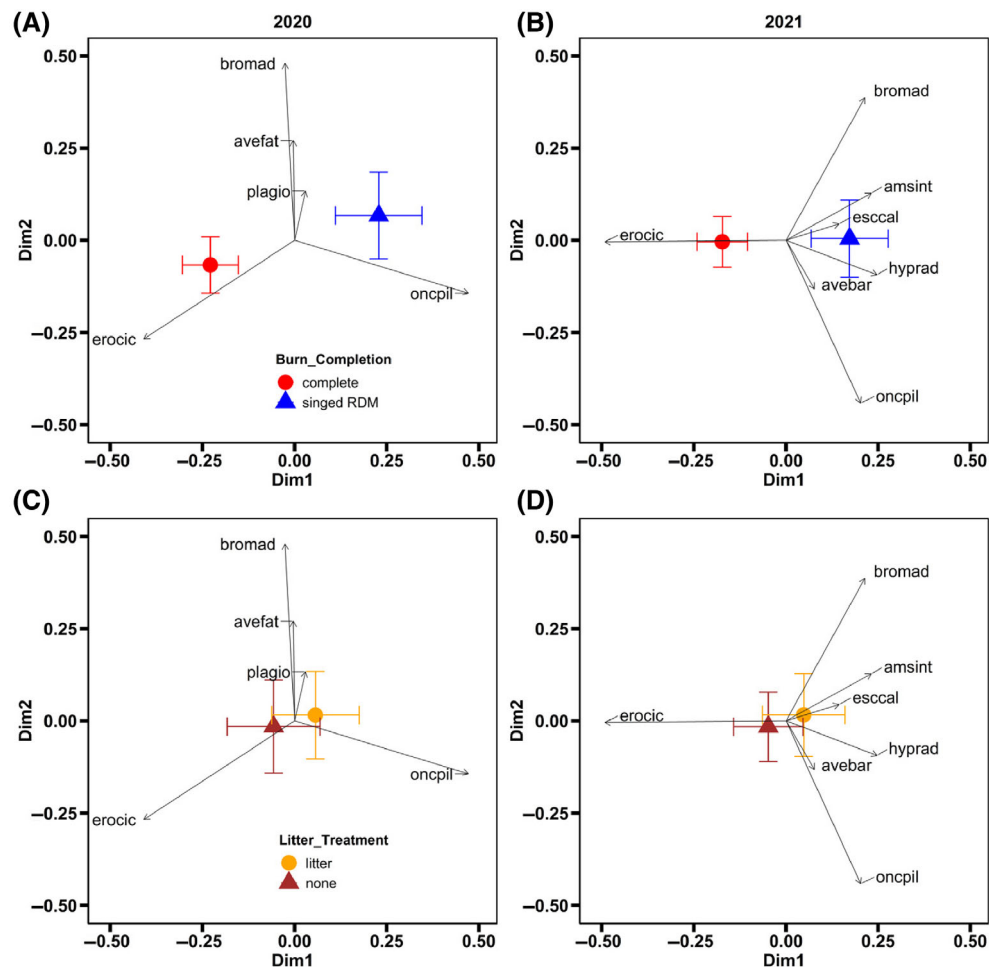


Figure 4. Principal coordinates analysis visualization of community level differences indicated by permutational analysis of variance (PERMANOVA). Points are average scores of every plot, and bars represent  $\pm$  95% CI. Species codes, full names, years present, and common names are listed in Table S1. (A) Effects of burn completion on community composition in 2020. (B) Effects of burn completion on community composition in 2021. (C) Effects of litter treatments on community composition in 2020. (D) Effect of litter treatment on community composition in 2021.

The singed stands had lower soil moisture and soil temperatures compared to the complete burn, and litter reduced soil temperatures as well as proportion of light. Invasive species often exhibit priority effects, where they may draw down resources earlier in the growing season that can have drastic impacts on community structuring and composition (Fukami 2015). In our experiment we had high invasive cover, and the environmental conditions that were measured during peak biomass, likely reflect the higher resource demands of the plants that survived the full growing season. Taking measurements earlier in the growing season may help elucidate to what extent differential resource use may impact the germination and establishment of other species. Although native species may benefit from ameliorated microclimate stresses through litter retention, the competitive interactions from non-native species with faster resource acquisition strategies may limit native performance (Amatangelo et al. 2008; Wainwright et al. 2011). Alternatively, litter can cause strong selection pressure to favor taller species due to light limitation (Harpole & Tilman 2007; Amatangelo

et al. 2008). Within California grasslands, grass litter has been shown to reduce native establishment (Molinari & D'Antonio 2020). *Oncosiphon* litter may similarly facilitate the dominance of *Oncosiphon* and *Bromus*, two fast growing species with vertical growth forms, while increasing native seedling mortality due to increased competitive pressures (Fenner & Thompson 2005; Harpole & Tilman 2007; Amatangelo et al. 2008). Additionally, litter presence exacerbates competitive differences and can negatively impact both resource acquisition and resource conservative native species (LaForgia 2021). Thus, the potential beneficial impacts of litter on native species establishment in xeric areas postburn may be dependent upon the density of litter and the environmental or biotic stressors driving seedling mortality.

In addition to the microclimate differences, seed availability in the postburn landscape is a major driver of postburn establishment. Initial flushes of native species postfire are often overwhelmed by reinvasion of well-established invaders coming from surrounding areas (Dickens & Allen 2009; Alba

et al. 2014). We observed that remaining singed stands acted as reservoirs of invasive seed, forming an in situ source of invader seed within burn areas. Increased seed availability postfire has been demonstrated to facilitate invader spread and alter recovery trajectories of grasslands (Dickens & Allen 2009; Gioria et al. 2012). In our study, singed stands had both greater *Oncosiphon* cover and more than double the amount of *Oncosiphon* seeds. More work is needed to explore whether any residual *Oncosiphon* seed benefits from increased germination rates postburn, which may exacerbate refugia dynamics. In our community level analysis, *Bromus* and *Oncosiphon* both had greater dominance with litter and in singed stands. The high cover of non-native species like *Oncosiphon* and *Bromus* within singed stands and with litter added suggests that these species were able to better capitalize on the ameliorated conditions of the litter and singed stands and both benefitted from retention of seed. Such establishment of invaders postcontrol efforts (i.e. secondary invasions) have been demonstrated as a key factor limiting management outcomes (O'Loughlin & Green 2017) as non-native species are often more able to take advantage of increases in resource availability (Wainwright et al. 2011) in the postmanagement landscape (D'Antonio & Meyerson 2002). The singed stands might provide a refuge for invaders to form in situ satellite subpopulations (Moody & Mack 1988) causing the reinvasion of burn areas to occur more rapidly than from surrounding seed rain alone. In this study, the singed stands within the postburn landscape had a small spatial footprint, taking up less than 20% of the full burn area in this experiment, and are highly visible within the burn area; therefore, we suggest that they could be a target for further restoration activities. Notably, the removal of satellite populations of the invader *Pennisetum ciliare* was found to reduce the doubling time of the invasion (Weston et al. 2019). Selectively spraying preemergent herbicide may further reduce the potential for reinvasion (Lazarus & Germino 2022). The source of invader seed as either surrounding propagule pressure or in situ survival of seeds in singed stands may be best elucidated by remote sensing, as this technique allows for spatial analysis of spread within treatment areas (Park et al. 2018; Dash et al. 2019). Our study demonstrates the importance of postburn heterogeneity and a mechanism from which invaders may spread within a prescribed burn; however, long-term studies as well as remote sensing may be required to determine the rate and extent of this mechanism contributing to postburn recovery and the full impacts on native establishment.

We predicted that native species would be seed limited, but as in many other studies (e.g. Suding & Gross 2006; Tognetti & Chaneton 2012; James et al. 2013) we observed a limited response from our native seed addition efforts. A lack of symbiotic partners (Vogelsang & Bever 2009), combined with competitive pressures from invasives (Pearson et al. 2016), and anthropogenic changes like nitrogen deposition (Vallano et al. 2012) might be too great of an obstacle for native species establishment and persistence. Moreover, these factors may interact to create barriers to native species establishment (Sigüenza et al. 2006; Larios & Suding 2015). Barriers to native establishment such as the lack of symbionts (Vogelsang &

Bever 2009) may require inoculations to improve native establishment as other studies have shown (e.g. Middleton & Bever 2012; Koziol & Bever 2017). Invasive allelopathic litter can further drive reductions in native performance through preventing germination (Loydi et al. 2015); however, there have not been any published studies on the potential allelopathic effects of *Oncosiphon* litter. Despite the general low native species cover, even with seed addition, our study highlights the need for additional management actions beyond seeding to increase native establishment.

Prescribed burns are an important vegetation management tool (Kimmerer & Lake 2001; Valkó et al. 2014; Valkó & Deák 2021) and, in many cases, can be effective for intended purposes of removing litter and invader seedbanks while increasing native establishment (Reynolds et al. 2001; Keeley et al. 2008; Dickens & Allen 2009). However, in the case of *Oncosiphon*, an invasive forb, burning leads to extensive heterogeneity that may result in rapid invader reestablishments. Future work should explore the flammability of this species and other invasive forbs to better understand the mechanisms that may result in more singed stands. Spatial heterogeneity can have substantial impacts on restoration outcomes (Baer et al. 2005; Suding 2011), and we have demonstrated that heterogeneity created by management actions can also drive substantial differences in recovery trajectories. The variation in restoration outcomes remains a major challenge (Brudvig et al. 2017); however, this challenge also provides an opportunity to elucidate ecological mechanisms mediating the efficacy of management efforts (Eviner & Hawkes 2008). Litter and seed consumption during fire are the underlying mechanisms driving the efficacy of prescribed burns, and forbs are not consumed in the same way as invasive grasses (Pyke et al. 2010). Our study highlights the potential for prescribed burning of invasive forbs to create a network of residual stands that facilitate reinvasion.

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## Supporting Information

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

**Figure S1.** Seeded species responses in the field.

**Figure S2.** Principal coordinates analysis visualization of community level differences indicated by permutational analysis of variance.

**Table S1.** Species present in field sampling.

**Table S2.** Species present in seedbank study.

**Table S3.** Average vegetative cover and standard error of seeded species recruitment in seeded and unseeded treatments.

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