FIRE REGIMES IN DESERT ECOSYSTEMS: DRIVERS, IMPACTS AND CHANGES

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Editorial: Fire regimes in desert ecosystems: Drivers, impacts and changes

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Editorial on the Research Topic
Fire regimes in desert ecosystems: Drivers, impacts and changes

Introduction

Although not commonly associated with fire, many desert ecosystems across the globe do occasionally burn, and there is evidence that fire incidences are increasing, leading to altered fire regimes in this biome. The increased prevalence of megafires (wildfires >10,000 ha in size and typically damaging) in most global biomes is linked to climate change, although those occurring in deserts have received far less attention, from both a research and policy perspective, than that of forested ecosystems (Linley et al., 2022). Understanding the drivers of desert fires, from climate to landscape patterns of hydrology and soil, and how these may be changing in the face of anthropogenic pressures, such as invasive species, livestock grazing, and global climate change, is imperative. This Research Topic has published nine papers addressing these drivers, how they have changed, and their impacts on desert biodiversity.

Role of invasive grasses and ecosystem transitions

Deserts are typified by sparse, discontinuous vegetation which has resulted in historically infrequent fire and low resilience of native vegetation, particularly shrubs and trees. Invasive grasses can increase the amount, continuity, and ignitability of fuelbeds, resulting in increased occurrence of fire (D'Antonio and Vitousek, 1992). Increased fire occurrence can cause type-conversions of native desert vegetation to non-native invasive grassland (Brooks et al., 2004).

Rodhouse et al. demonstrated this type-conversion dynamic with the invasive annual grasses *Bromus tectorum* and *Taeniatherum caput-medusae* at a North American Cold Desert site. They also reported that native perennial grasses can be more resilient than woody species to fire and used that finding to develop site-specific conservation recommendations. Wilder et al. explained how the invasive annual grass *Bromus rubens* and perennial grass *Cenchrus ciliaris* are altering fire regimes in a North American Warm Desert region. They also explain how this threatens both human communities at the wildland urban interface (WUI) and higher elevation native forest communities which are otherwise somewhat resilient to fire. Moloney et al. provides an example of how fire potential can be modeled by characterizing the matrix of patchy native perennial fuels connected across interspaces by more continuous invasive annual grass fuels.

Spatial patterns of fires and fire regimes

Remote sensing data collected by satellites and aircraft are now routinely used to detect active fires and map fire scars accurately and efficiently; analysis of these data can determine many components of the fire regime, and how these have changed over time, providing valuable insights and a sound basis for fire management, from global (Chuvieco et al., 2008) to local (e.g., Verhoeven et al., 2020) scales. Such techniques are particularly suited to arid and semi-arid lands given their general remoteness and vastness (Ruscalleda-Alvarez et al., 2021).

Clarke et al. and van Etten et al. used such mapped fire scars to effectively characterize fire regimes of two semi-arid regions of southern Australia. Periodic, intense, and stand-replacing wildfires were of over-riding importance in shaping the fire regimes in both regions, creating mosaics of different fire ages across the landscape, including many long unburnt patches. This combined with slow recovery of vegetation after burning, resulted in generally long intervals between fires. van Etten et al. demonstrated highly contrasting fire regimes across landscapes linked to soil/vegetation type, whilst Klinger et al., using remote-sensing derived maps of fire frequency and severity, also found spatially-structured fire regimes across the Mojave desert.

Climate-fire interactions

Wildfires in semi-arid and arid zones are often driven by rainfall-led increases in fuel loads, rather than droughts that increase the flammability of vegetation in more mesic regions (McLauchlan et al., 2020). Clarke et al. reviewed the role of wildfire in contemporary mallee ecosystems, with particular focus on south-eastern Australia. They found that wildfires occur in late spring and summer in both dry and wet years. Annual rainfall is sufficient to maintain vegetation and fuel connectivity within and across years. Fire return intervals are 10–20 years, but fires can return sooner after high rainfall events. In contrast van Etten et al. demonstrated that wildfire in a semi-arid region of inland south-western Australia was strongly linked with high rainfall in the year prior to fire and had longer fire return intervals from 25 and 100 years. The differences in fire regimes between the two mallee systems may be due to lower rainfall in south-western Australia. In arid regions of North America and Australia, both Brunelle and Wright et al. found a strong association between antecedent rainfall and wildfire. Brunelle examined paleoenvironmental records and found an increase in fires after the emergence of El Nino events (after ~4,500 cal yr BP), which influences winter rainfall events in North American desert southwest. Wright et al. investigated a range of different sources—from explorer diaries and remote sensed data—to show that large-scale wildfires occurred after high-rainfall events in spinifex grassland in the Western Desert of Australia, regardless of previous fuel management practices. In common across both semi-arid and arid regions investigated above, these ecosystems experience megafires and changing rainfall regimes due to climate change may have profound effects on fire regimes in these ecosystems.

Species responses to fire

Understanding species responses to fire(s) is important in predicting the fate of populations following burning; adaptations to withstand or recover following fire are generally expected to be less strongly developed in arid zones compared to more fire-prone biomes. Saguaro (*Carnegiea gigantea*), the giant columnar cactus of the Sonoran Desert, as well as many other cacti, experienced high mortality and no to minimal resprouting following a particularly severe wildfire event studied by Wilder et al., with smaller plants being more susceptible. In contrast, many other plants, including the dominant shrubs, demonstrated high resprouting capacity following fire, suggesting pre-adaptation to fire, possible as a response to other stresses, such as drought. St Clair et al. specifically studied regeneration of Joshua trees (*Yucca jaegeriana*) following wildfires in the Mojave Desert and reported variable degrees of resprouting, mostly from the base of trees, but little regeneration from seed.

Clarke et al. presented a synthesis of many studies done over several years; consequently, they were able to report responses to fire regimes, as opposed to single fire events. They found many understory plant species in semi-arid south-east Australia were obligate seeders regenerating from the soil seed bank after fire, but were vulnerable to repeated fires, whereas the dominant overstory mallees (multi-stemmed *Eucalyptus*) and many of the dominant hummock grasses (*Triodia* spp.) resprouted from below-ground structures. With change in vegetation over time, abundances of the studied animal species (including birds, reptiles and small mammals) also changed. Clarke et al. classified responses of these fauna into six categories, depending on if, and when, their abundances peaked post fire.

Conclusions and closing comments

The various papers in this Research Topic have demonstrated that shifting fire drivers are leading to altered fire regimes in many desert ecosystems, and that we need to be particularly concerned with synergistic effects of these drivers, such as climate changes interacting with invasive grasses to produce more frequent, hotter, and larger wildfires. The impending threats of changing fire regimes on biodiversity require an enhanced research agenda, particularly in desert regions outside of southwestern USA and inland Australia (where all the studies in this Research Topic were based).

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Conflict of interest

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References

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., et al. (2004). Effects of invasive alien plants on fire regimes. *Bioscience.* 54, 677–688. doi: 10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Chuvieco, E., Giglio, L., and Justice, C. (2008). Global characterization of fire activity: towards defining fire regimes from Earth observation data. *Glob. Change Biol.* 14, 1488–1502. doi: 10.1111/j.1365-2486.2008.01585.x

D'Antonio, C. M., and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87. doi: 10.1146/annurev.es.23.110192.000431

Linley, G. D., Jolly, C. J., Doherty, T. S., Geary, W. L., Armenteras, D., Belcher, C. M., et al. (2022). What do you mean, 'megafire'? *Global Ecol. Biogeogr.* 1–17. doi: 10.1111/geb.13499

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., et al. (2020). Fire as a fundamental ecological process: research advances and frontiers. *J. Ecol.* 108, 2047-2069. doi: 10.1111/1365-2745.13403

Ruscalleda-Alvarez, J., Moro, D., and Van Dongen, R. (2021). A multi-scale assessment of fire scar mapping in the Great Victoria Desert of Western Australia. *Int. J. Wildland Fire.* 30, 886–898. doi: 10.1071/WF21019

Verhoeven, E. M., Murray, B. R., Dickman, C. R., Wardle, G. M., and Greenville, A. C. (2020). Fire and rain are one: extreme rainfall events predict wildfire extent in an arid grassland. *Int. J. Wildland Fire.* 29, 702–711. doi: 10.1071/WF19087

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Post-Fire Vegetation Response in a Repeatedly Burned Low-Elevation Sagebrush Steppe Protected Area Provides Insights About Resilience and Invasion Resistance

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Sagebrush steppe ecosystems are threatened by human land-use legacies, biological invasions, and altered fire and climate dynamics. Steppe protected areas are therefore of heightened conservation importance but are few and vulnerable to the same impacts broadly affecting sagebrush steppe. To address this problem, sagebrush steppe conservation science is increasingly emphasizing a focus on resilience to fire and resistance to non-native annual grass invasion as a decision framework. It is well-established that the positive feedback loop between fire and annual grass invasion is the driving process of most contemporary steppe degradation. We use a newly developed ordinal zero-augmented beta regression model fit to large-sample vegetation monitoring data from John Day Fossil Beds National Monument, USA, spanning 7 years to evaluate fire responses of two native perennial foundation bunchgrasses and two non-native invasive annual grasses in a repeatedly burned, historically grazed, and inherently low-resilient protected area. We structured our model hierarchically to support inferences about variation among ecological site types and over time after also accounting for growing-season water deficit, fine-scale topographic variation, and burn severity. We use a state-and-transition conceptual diagram and abundances of plants listed in ecological site reference conditions to formalize our hypothesis of fire-accelerated transition to ecologically novel annual grassland. Notably, big sagebrush (*Artemisia tridentata*) and other woody species were entirely removed by fire. The two perennial grasses, bluebunch wheatgrass (*Pseudoroegneria spicata*) and Thurber's needlegrass (*Achnatherum thurberianum*) exhibited fire resiliency, with no apparent trend after fire. The two annual grasses, cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*), increased in response to burn severity, most notably medusahead. Surprisingly, we found no variation in grass cover among ecological sites, suggesting fire-driven homogenization as shrubs were removed and annual grasses became dominant. We found contrasting responses among all four grass species along gradients of topography and water deficit, informative to protected-area conservation strategies. The fine-grained influence of topography was particularly important to

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variation in cover among species and provides a foothold for conservation in low-resilient, aridic steppe. Broadly, our study demonstrates how to operationalize resilience and resistance concepts for protected areas by integrating empirical data with conceptual and statistical models.

Keywords: biological invasion, bluebunch wheatgrass, cheatgrass, fire, medusahead, national parks, sagebrush steppe, water balance

INTRODUCTION

Sagebrush steppe ecosystems across western North America have been lost or degraded by cumulative impacts of human land-use legacies, biological invasions, and altered fire and climate dynamics (Davies et al., 2011). Steppe protected areas are therefore of heightened conservation importance but are few in number (Caicco et al., 1995; Noss et al., 1995; Stoms et al., 1998) and vulnerable to many of the same cumulative impacts broadly affecting sagebrush steppe. To address this problem, sagebrush steppe conservation science is increasingly emphasizing a focus on resilience to fire and resistance to non-native annual grass invasion as a decision framework (e.g., Chambers et al., 2019), now that it is well-established that the positive feedback loop between fire and annual grass invasion is the driving process of most contemporary steppe degradation (D'Antonio and Vitousek, 1992; Brooks et al., 2004; Chambers and Wisdom, 2009; Balch et al., 2013). Resilience to fire, which is defined as site capacity to return to pre-fire structure and function (e.g., native perennial grass cover is recovered over time), and the annual grass invasion resistance of sagebrush steppe ecosystems varies predictably along topographic-moisture gradients (Chambers et al., 2014a). The position of steppe landscapes along these gradients can be used to guide conservation decision-making (e.g., Chambers et al., 2014b). For example, high elevation (e.g., 1,500 m) steppe with mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) overstory tends to be much less invasible by annual grasses of Eurasian origin than low elevation (e.g., <1,000 m) steppe with Wyoming and basin big sagebrush (*A. t.* subsp. *wyomingensis* and *A. t.* subsp. *tridentata*) overstories (Chambers et al., 2014a). Low-elevation, low-productivity sites exhibit higher inertia and are much more difficult and expensive to restore (Suding et al., 2004; James et al., 2013), and when considered from a regional strategic perspective, high-elevation sites may therefore be considered as being of higher conservation priority (Chambers and Wisdom, 2009; Chambers et al., 2019). However, this confronts those low-elevation protected-areas that exhibit inherently low resilience to fire and resistance to invasion with an existential challenge requiring pro-active strategic landscape prioritization and triage. To fail to do so will likely result in the loss of low-elevation steppe protected areas as places of conservation value given current trajectories of degradation.

Like all protected areas, those in low-elevation sagebrush steppe are fixed in geographic space even as the ecological gradient space within which they occur (e.g., temperature and precipitation, fire regime) shifts over time toward novel conditions with less native biodiversity and lower conservation value. For example, National Park Service sites containing sagebrush steppe across the Columbia Basin and Snake River Plain have all experienced substantial fire-induced shifts toward novel annual grasslands in recent decades (Bangert and Huntly, 2010; Ellsworth and Kauffman, 2010; Powell et al., 2013; Rodhouse et al., 2014; Reed-Dustin et al., 2016; Esposito et al., 2019; Ellsworth et al., 2020; Nicolli et al., 2020), yet each of these parks are also charged with preserving native steppe as established by the 1916 National Park Service Organic Act. In order to meet this charge, these parks and others faced with the same kinds of challenges to protected-area relevancy need to develop granular, place-based ecological insights that are useful for park-scale preservation and restoration planning and contextualized within the resilience and resistance framework.

Inferences and predictions from statistical models fueled by field and remotely sensed observations can be an effective way to support park-specific evidence-based conservation decision-making, particularly when integrated into adaptive management supported by recurring monitoring. For example, Rodhouse et al. (2014) used field-based monitoring data and statistical regression to predict where native foundation bunchgrasses were most likely to occur along topographic gradients within the John Day Fossil Beds National Monument (JODA) in north-central Oregon, USA. These predictions were inferred to indicate apparent resilience and resistance and used to prioritize implementation of park burned-area emergency response and weed management plans (Hoh et al., 2015). More recently, the soil and ecological site attributes provided by the US Natural Resource Conservation Service (NRCS) web soil survey have been used to map current and future potential resilience and resistance across the sagebrush steppe biome (Maestas et al., 2016; Bradford et al., 2019), including in protected areas. For example, each of the separate management units of JODA are mapped almost entirely as low resilience currently and in the future (**Figure 1A**), a predicament also faced by other parks in the region. The mappable linkages between soil surveys and potential resilience and invasion resistance creates important opportunities to operationalize these concepts into a decision-making framework. However, it is evident that the generalized assessments by Bradford et al. (2019, e.g., **Figure 1A**) and others will need to be empirically evaluated and translated with more granularity and precision for park operations.

To support this need, we evaluate a 7-year (2011–2017) study of native and non-native grass species' responses to a 2011 wildfire in a repeatedly burned and inherently low resilience protected-area landscape in the John Day Fossil Beds National Monument. We use a newly developed class of zero-augmented

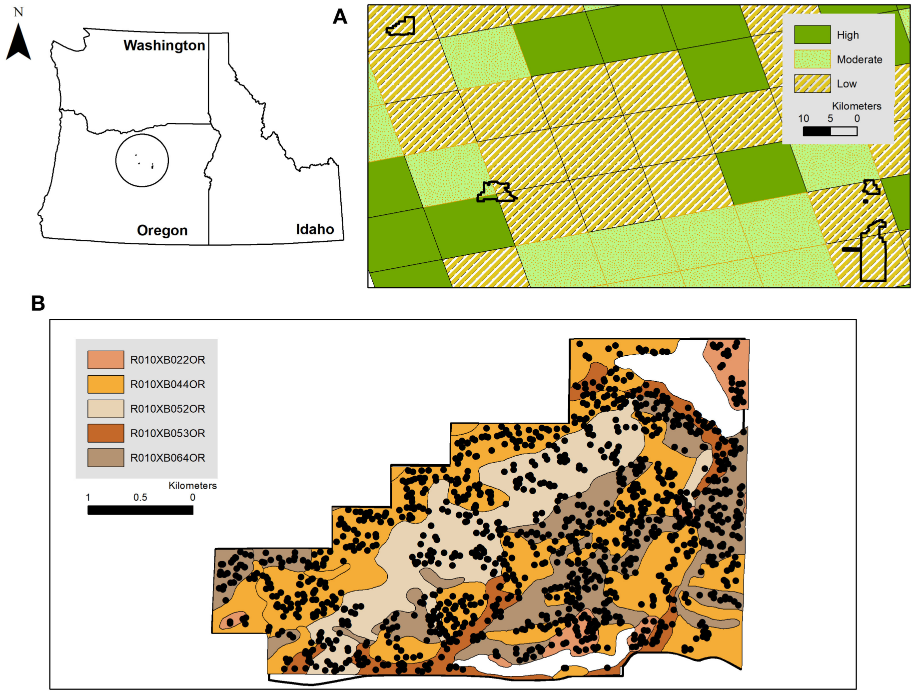

FIGURE 1 | (A) The five units of the John Day Fossil Beds National Monument, including Clarno (upper left) mapped to the current ecological resilience predictions developed by Bradford et al. (2019). Note that future resilience in this region (upper left **A**) was predicted to remain low under climate change scenarios examined by Bradford et al. (2019). **(B)** The five ecological sites in Clarno (John Day Fossil Beds National Monument) mapped by Natural Resources Conservation Service Web Soil Survey for the National Park Service (NPS, 2012) overlain with vegetation monitoring quadrat locations surveyed during 2011–2017 following a National Park Service protocol (Yeo et al., 2009). Inset shows the position of the John Day Fossil Beds National Monument within Oregon, USA.

ordinal regression (Irvine and Rodhouse, 2010; Irvine et al., 2016, 2019) to model variation in quadrat-based observations of above-ground grass cover categories over time since fire and in relation to ecological site, topographic position, fire severity, and growing-season (October-May preceding each field survey) water deficit. The zero-augmented (hurdle-at-zero) model approach allowed us to explicitly evaluate patterns in occurrence (presence/absence) and in abundance (cover categories >0) simultaneously. We structured our model hierarchically so that observations could be grouped within ecological sites, an important step in contextualizing model-estimated trends over space and time within the resilience and resistance framework. We used the same ecological site descriptions developed through the NRCS web soil survey (NPS, 2012) as was used by Bradford et al. (2019) to develop their regional resilience and resistance map, although we retained the NRCS soil survey map unit polygons (see **Figure 1B**) rather than the coarse grid employed by Bradford et al. (2019). Importantly, we were able to utilize attributes of the ecological sites, including associated state-and-transition diagrams (*sensu* Stringham et al., 2003; Chambers et al., 2014c) and reference plant species lists as articulated hypotheses about fire-driven state transitions (**Figure 2**). Specifically, we hypothesized that the entire study area would exhibit accelerated transition to the annual grass state (state 3, **Figure 2**) because of the 2011 fire and earlier observations about shrub cover loss from previous burns, but with variation in that transition among ecological sites as a result of topographically-mediated effective soil moisture and site productivity that confers relative resilience and invasion resistance.

We used the models to examine cover patterns of two large-stature native foundational bunchgrass species and two invasive annual grasses of Eurasian origin. The two perennial species, bluebunch wheatgrass (*Pseudoroegneria spicata*; wheatgrass, hereafter) and Thurber's needlegrass (*Achnatherum thurberianum*; needlegrass, hereafter), comprise >75% of the total plant community biomass of the hypothetical historic reference state (state 1) in **Figure 2** (NRCS citation), and ~10% of the biomass in the invaded state (state 2 in **Figure 2**). The two annual grasses that we examined, cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*), are the dominant invasive species associated with both the invaded state and the annual grass state (states 2 and 3 in **Figure 2**). The relative abundances of these four species are therefore useful indicators of these hypothesized states described in **Figure 2** and of resilience to fire and resistance to annual grass invasion for this study area, more generally. The inferences supported by our statistical survey design and our models provide insights about resilience and resistance that will support a more strategic approach to park steppe conservation than what has been pursued previously, specifically revealing the importance of topography in our study area as a strong mediator of resilience and resistance which can provide a conservation foothold. More generally, our approach demonstrates the importance of using empirical data and both conceptual and statistical models in

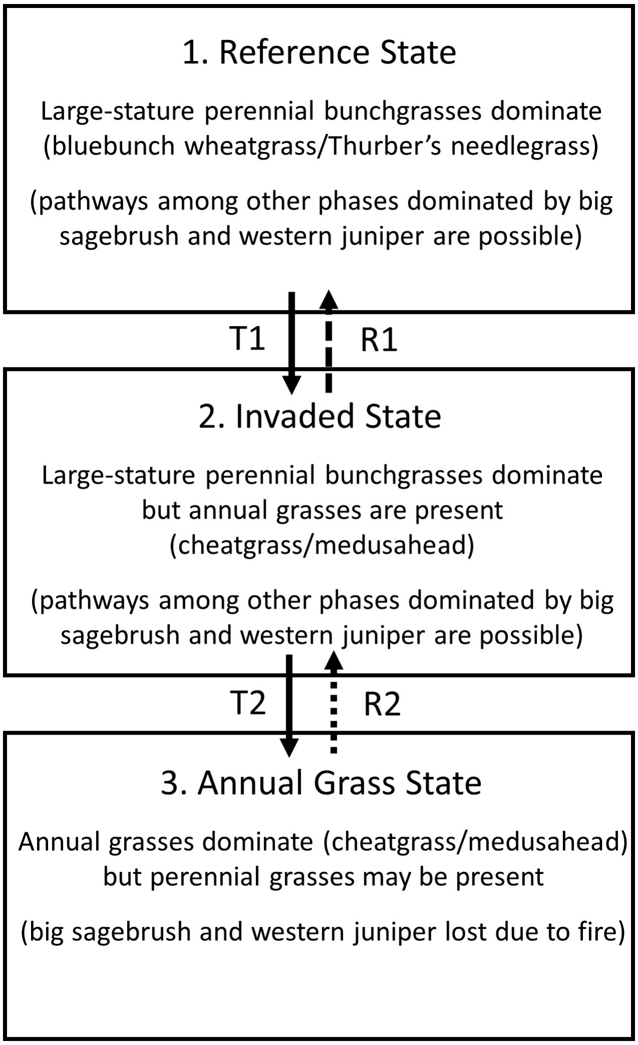

FIGURE 2 | A simplified state-transition diagram for the aridic low-elevation sagebrush steppe ecological sites within the Clarno unit of the John Day Fossil Beds National Monument, modified from Natural Resources Conservation Service ecological site descriptions (NPS, 2012), Chambers et al. (2014c), and Ellsworth et al. (2020). This diagram highlights three fundamental states with progressively steep threshold transitions into ecologically-novel conditions dominated by invasive annual grasses, from state 1 to state 2 and from state 2 to state 3. Note that other phases within these states dominated by big sagebrush and western juniper are possible (NPS, 2012; Chambers et al., 2014c; Ellsworth et al., 2020) but were not observed during our study due to past wildfires.

an integrated way to operationalize resilience and resistance concepts for place-based conservation decision-making in an increasingly at-risk North American biome.

MATERIALS AND METHODS

Study Area

We evaluated post-fire response of native and non-native grasses over a 7-year period from 2011 to 2017 in the Clarno Unit of the John Day Fossil Beds National Monument, in north-central Oregon, USA (**Figure 1**). The Clarno Unit encompasses 5,800 ha of upland sagebrush steppe. Elevations range from 421 to 725 m. Clarno is topographically rugged, comprised of highly weathered volcanic ash-derived clay to stony clay-loam soils. Thirty-year mean annual precipitation is ∼27 cm (ecological sites are attributed to 22–30 cm precipitation zones), and precipitation falls mostly as rain and ephemeral snow during October to May, which drives the growing season for the four cool-season grasses examined. Wildfires occurred in the study area in 1985, 1994, 1995, and 2011 (**Supplementary Figure 1.1**), and we assumed that all quadrat locations experienced at least 2 burns within this time period, although lack of a published perimeter for the 1985 fire and variation in burn severity make it difficult to establish exact fire history. This fire history represents an ∼10–20-year fire frequency, which is substantially shorter than the multi-decadal to centuries intervals established for low-elevation aridic Wyoming and basin big sagebrush ecosystems (e.g., Chambers and Wisdom, 2009; Bukowski and Baker, 2013).

Historically, Clarno was grazed by sheep and cattle for many decades prior to establishment as a National Park Service unit and effective fencing was constructed. Without quantitative information on grazing history (e.g., variation in timing and duration within the study area), however, it was impossible to account for land-use legacy in the study. Nonetheless, this legacy is an important aspect to the unfolding story of environmental change in the Monument and contextualizes our results.

Sagebrush steppe plant communities in Clarno were mapped prior to the 2011 wildfire by Erixson et al. (2011) following the National Vegetation Classification System to include ∼20% Wyoming-type sagebrush steppe (dominated by *A. t.* subsp. *wyomingensis*) and >50% as herbaceous, dominated by large-stature native perennial bunchgrasses (wheatgrass and needlegrass) or invasive annual grasses (cheatgrass and medusahead; **Supplementary Figure 1.2**). Western juniper (*Juniperus occidentalis*) trees were present in open savannah along several drainage bottoms. Five ecological sites were mapped in the study area by NRCS (NPS, 2012; **Figure 1B**), each of which share important abiotic attributes that pre-dispose the entire study area to inherently low resilience to fire and resistance to invasion, most importantly shared mesic soil temperature and aridic soil moisture regimes (Chambers et al., 2014a; Maestas et al., 2016; Bradford et al., 2019). The state 1 (**Figure 2**) reference conditions for each of the ecological sites list basin big sagebrush (*A. t.* subsp. *tridentata*) as the dominant shrub, although Wyoming big sagebrush was more common on these sites, as mapped by Erixson et al. (2011). Differences among ecological sites include two (ecological sites R010XB022OR and R010XB064OR) that were characterized as north-facing slopes dominated by wheatgrass more than needlegrass, and three (R010XB044OR, R010XB052OR, R010XB053OR) predominantly south-facing slopes dominated primarily by needlegrass. Notably, topographic heterogeneity measured from a 10-m digital elevation model was much greater than indicated by ecological site descriptions, and each ecological site included relatively wide gradients of slopes and aspects (**Supplementary Figures 1.3–1.5**).

Field Sampling Methods

We used vegetation monitoring data collected in the Clarno Unit of the John Day Fossil Beds National Monument during 2011–2017 as part of the National Park Service's vital signs monitoring program (Fancy et al., 2009). Field methods followed a protocol (Yeo et al., 2009) for ocular estimation of above-ground foliar cover categories of plant species found within 1-m^2 quadrats, following Daubenmire (1959) 7-level system (including a 0 cover class; 0% = 0, >0–5% = 1, >5–25% = 2, >25–50% = 3, >50–75% = 4, >75–95% = 5, and >95% = 6). Quadrats were randomly located in the field following a spatially-balanced equal probability randomization (the Generalized Random Tessellation Stratified [GRTS] algorithm, Stevens and Olsen, 2004). We used the R library *spsurvey* (Kincaid and Olsen, 2019) to implement GRTS sampling. The GRTS design ensures spatial balance and representativeness of the sample within the area of inference (i.e., the sample frame) and has advantages over alternative approaches such as simple random and stratified random sampling that include more efficient design-unbiased population variance estimation, spatial balance, and reduction in autocorrelation, and flexibility for replacing sample units (Stevens and Olsen, 2004). Randomization was constrained within a sampling frame constructed in a GIS from vegetation maps that included all upland vegetated areas <30 degrees (58%) slope and that also excluded barren fossil-bearing ash beds that are sensitive to trampling (**Supplementary Figure 1.2**). Steep slopes >30 degrees presented safety risks to field observers and represented a relatively small amount of land removed from the sampling frame (**Supplementary Figure 1.2**). New independent random samples were drawn each year. Quadrats were not permanently marked and never revisited (a "never-revisit design" *sensu* Urquhart and Kincaid, 1999; MacDonald, 2003). The Monument discouraged use of permanent markers (e.g., steel rebar) but large independent samples each year offset the potential loss of power from not using permanent plots. Sample sizes ranged from 85 to 211 annually, totaling 1,338 quadrat observations (**Table 1**). Sample sizes were informed by a statistical power analysis developed specifically for the protocol, and examined via simulations (Irvine and Rodhouse, 2010; Irvine et al., 2016). Our annual samples covered the complete ranges, means, and standard deviations of the environmental gradients (slope, aspect, elevation) within the sample frame. In all years but 2012, our achieved sample sizes were twice the size recommended ($\sim n = 100$) by Irvine and Rodhouse (2010). Surveys were conducted annually in early June, and species cover was visually assessed and binned into Daubenmire categories. Data are available on-line at: https://irma.nps.gov/DataStore/Reference/Profile/2278547.

Statistical Analyses

We summarized plant species cover by plotting stacked bar charts with the proportion of quadrats in each cover class. The empirical proportion, $\hat{p} = \frac{x}{n}$, is a design-unbiased population estimator for categorical data (Agresti, 2010). We used a multi-level (hierarchical) ordinal zero-augmented beta regression (OZAB; Irvine et al., 2016) to examine the patterns of cover, in Daubenmire categories, along gradients of topography, fire severity, growing season water deficit, time (year), and ecological site. The OZAB model specifies a more flexible latent beta distribution to model plant cover (Damgaard and Irvine, 2019) rather than a latent logistic distribution as is done with the more familiar proportional-odds logistic regression (POLR; Agresti, 2010). An important distinction between OZAB and POLR is the ability to use the more flexible 2-parameter beta distributions to remove the restrictive assumption that the odds of moving into a higher plant cover category is the same between all categories. Adding a hurdle-at-zero model adds additional flexibility and the OZAB model provides an integrated framework to explore both presence/absence and abundance patterns and processes (Irvine et al., 2016). Furthermore, the OZAB model directly links the cover classes to the partially-observed latent percent cover, allowing model parameters (e.g., environmental gradient coefficients) to be interpreted in terms of changes in mean percent cover rather than in terms of cumulative odds ratios, which are not intuitive (Irvine et al., 2016). The OZAB model provides more precise parameter estimates than POLR or when using linear regression with category midpoints (Irvine and Rodhouse, 2010; Irvine et al., 2016). We reported the unconditional mean cover (and 95% credible intervals), as a proportion, among years and ecological sites, for each species.

Following, Irvine et al. (2016, 2019), the observed cover categories were treated as a grouped continuous ordinal response from a multinomial distribution with J + 1 categories, $[C_i|\pi_i] = Multinomial(1, \pi_{0i}, \ldots, \pi_{Ji})$, for $i = 1, \ldots n$ observations (quadrats or plots) with category levels of 0, 1, ..., J and $\Pr\left(C_i = j\right) = \pi_{ji}$. The key advantage of the OZAB approach is specifying the latent variable (Y_i^*) distribution as a mixture of a continuous beta distribution and a point mass at 0, as follows:

$$\left[Y_i^*|\alpha, \mu, \phi\right] = \begin{cases} 1-\alpha, & \text{if } Y_i^* = 0 \\ (\alpha)\,[Y_i|\mu, \phi], & \text{if } Y_i^* \in (0, 1) \end{cases}$$

where $\left[Y_i^*|\alpha, \mu, \phi\right]$ is the zero augmented beta distribution. The abundance portion of the model was parameterized for regression by Ferrari and Cribari-Neto (2004) with $E\left(Y_i\right) = \mu$ and $Var\left(Y_i\right) = \frac{\mu(1-\mu)}{\phi+1}$. For the plant cover class data used in this study, μ is interpreted as the mean proportion cover conditional on presence. The unconditional mean cover is estimated by $\alpha\mu$.

The observed cover class category was defined as a discretized version of Y_i^* for observation i as follows:

$$C_i = \begin{cases} 0, \text{if and only if } Y_i^* = 0 \\ j, \quad \text{if and only if } \theta_{j-1} < Y_i^* \leq \theta_j \; for \; j = 1, \ldots, J \end{cases}$$

where $\boldsymbol{\theta}$ represents the breaks between each cover class. The Daubenmire (1959) scale defines the vector as $\{\theta_0, \ldots, \theta_6\} = \{0, 0.5, 0.25, 0.5, 0.75, 0.95, 1.0\}$. The multinomial probabilities are:

$$\pi_{ij} = \begin{cases} 1-\alpha & j = 0 \\ \alpha \times F_{Beta}\left(\theta_1\right) & j = 1 \\ \alpha \times \left(F_{Beta}\left(\theta_j\right) - F_{Beta}\left(\theta_{j-1}\right)\right) & 2 \leq j \leq (J-1) \\ \alpha \times \left(1 - F_{Beta}\left(\theta_{j-1}\right)\right) & j = J \end{cases}$$

TABLE 1 | Sample sizes achieved during monitoring each year by ecological site, Clarno, John Day Fossil Beds National Monument.

Ecological site	2011	2012	2013	2014	2015	2016	2017	Total
R010XB022OR (22)	21	10	11	9	12	10	13	86
R010XB044OR (40)	82	33	89	91	92	93	87	567
R010XB052OR (52)	30	7	30	29	26	32	31	185
R010XB053OR 53)	34	10	20	16	27	16	22	145
R010XB064OR (64)	42	25	58	62	54	59	55	355
Total	209	85	208	207	211	210	208	1,338

The last two digits (in parentheses) of the ecological site alphanumeric code used by the Natural Resources Conservation Service is used in ***Figures 4***, ***5*** *for brevity.*

Where F_{Beta} denotes the cumulative distribution function for the partially observed conditional percent cover Y, which is beta distributed with parameters μ and ϕ.

The mean of proportion cover (μ) and probability of occurrence (α) were allowed to be influenced by explanatory variables (environmental gradient covariates) by using $logit\,(\mu_i) = X_i\beta$ and $logit\,(\alpha_i) = W_i\gamma$, where **X** and **W** represent a matrix of covariates obtained for each plot (Irvine et al., 2016). Continuous variable covariates were input as mean-centered and standardized quantities and categorical variable covariates were input as factors anchored at level 0 (e.g., unburned and study year 1) which facilitated computation and interpretation of μ and α. We specified diffuse normal priors on regression coefficients for γ ($[\gamma] = Normal\,(0, 0.01)$). Diffuse normal priors on abundance regression parameters β $\left([\beta] = Normal\,(0, 0.01)\right)$ and a diffuse Gamma prior for the precision parameter ($[\phi] = Gamma\,(0.1, 0.1)$) were also specified.

Environmental Gradients for Model Covariates

We used a 10-m digital elevation model (US Geological Survey National Elevation Dataset, http://ned.usgs.gov/) to obtain a measure of topography for each plot by calculating sin(slope) × cos(aspect), producing a variable that ranged from −1 to 1 (**Supplementary Figures 1.3–1.5**). Steep south-facing slopes trend toward −1 and steep north-facing slopes trend toward 1. This and similar calculations have been widely used to approximate insolation (Stage, 1976; McCune and Keon, 2002) which can indicate topographically mediated variation in effective soil moisture. We estimated burn severity for the 2011 fire by comparing two Landsat images immediately before (August 17, 2011) and after (September 9, 2011) the fire and estimating delta normalized burn ratio (dNBR; **Supplementary Figure 1.6**; Keeley, 2009). We used the US Geological Survey (USGS) Earth Explorer (earthexplorer.usgs.gov) to order and acquire Landsat 5 (based on USGS availability) normalized burn ratio scenes provided as part of the USGS suite of Landsat Surface Reflectance-Derived Spectral Indices products (see Masek et al., 2006). The two scenes subtracted to produce a dNBR raster were radiometrically corrected by USGS and ranked as level 1 precision and terrain corrected product (L1TP) quality. We binned severity values into five relative rankings categories, from unburned to high severity (**Supplementary Figure 1.6**) following approximately the thresholds described by Keeley (2009) and Key and Benson (2006), but tuned to our study area by an examination of the empirical distribution of observed dNBR values in our study and finding breakpoints that would ensure sufficient sample size within each category for inclusion as a 5-level factor model covariate. Including burn severity as a factor improved model computation and interpretation in terms of severity level description.

Water deficit during the growing season for cool-season grasses, which in our study region occurs during October-May preceding each sampling season (e.g., see ecological site descriptions, NPS, 2012) was used as an additional model covariate (**Supplementary Figure 1.7**). Water deficit is calculated as potential evapotranspiration minus actual evapotranspiration, and is a parsimonious, integrative variable for use in statistical models with fundamental influence on plant growth and vegetation, particularly in arid regions (Stephenson, 1990; Dilts et al., 2015; Thoma et al., 2020). Water deficit is derived from Thornthwaite-type water balance equations (Thornthwaite and Mather, 1955) that describe water availability to plants, accounting for latitude and solar loading, temperature and precipitation, and soil moisture (holding capacity). Water deficit is a more mechanistic description of water stress on plants in arid lands than using temperature and precipitation alone, or drought indices such as normalized difference water index that only measure leaf water content (Stephenson, 1990, 1998; Lutz et al., 2010; Dilts et al., 2015; Thoma et al., 2016, 2020). For our study, water deficit was estimated by Thoma et al. (2020) for the National Park Service from Thornthwaite water balance equations calculated at daily time steps across the continental US at 1 km resolution, following methods developed by Thornthwaite and Mather (1955) but with modifications described by Lutz et al. (2010) and Thoma et al. (2020). The 1 km resolution was constrained by the required daily inputs of precipitation and temperature from the Daily Surface Weather and Climatological Summaries (Thornton et al., 2018; Daymet; https://daymet.ornl.gov/). October-May water deficit during our study was lowest (∼18 mm) in 2014 and highest (∼23 mm) in 2016 (**Supplementary Figure 1.7**).

Model Fitting

We used a Bayesian approach to fit OZAB models, using three chains and 5,000 iterations of Markov chain Monte Carlo (MCMC) algorithms within the JAGS software (Plummer, 2003), launched from R (R Core Team, 2019) using the rjags package (Plummer, 2019). Slight variations on the maximum likelihood estimations for β and γ were used to initialize the three chains, as well as the corresponding midpoint values on the proportion cover scale for the unobserved beta latent variable.

We developed a hierarchical (i.e., mixed-effects or partial pooling *sensu* Gelman and Hill, 2007) model structure, grouping quadrat cover observations by ecological site type and year, allowing for a unique coefficient to be estimated for each ecological site and year in order to reflect the survey design and support inferences over space (ecological site) and time. Covariate matrices for both occurrence and abundance included topography, burn severity, and water deficit. We added a quadratic parameter for topography to allow curvature in the modeled influence of topography on cover. Topography and burn severity varied over space at fine scales (10 m and 30 m, respectively) but not time (**Supplementary Figures 1.5, 1.6**). Water deficit varied coarsely (1 km) over space because of data resolution and because weather and climate are synoptic processes, and varied over time as a year effect, although deficit was not correlated with year (**Supplementary Figure 1.7**). Full models were fit for both the abundance and presence portions of the OZAB model for each species separately. Unconditional means and 95% credible intervals were estimated from the posterior distributions of the three MCMC chains.

In order to evaluate model performance, we fit models with 90% of the dataset (1,251 plots), holding 10% of the dataset for model checking. We conducted posterior predictive checks for each model by assessing discrepancy between observed data and predicted data and by calculating Kendall's τ to measure the degree of concordance between observed cover classes and the predicted cover classes.

RESULTS

Woody overstory species were already rare in the study area prior to 2011 due to past wildfires and were almost entirely removed by the 2011 fire. This can be seen in the pairs of photographs in **Supplementary Figure 1.8** that were taken at 2 locations within the study area in 1988 and 2012. In 2011, we estimated that frequency of occurrence (empirical proportion when cover >0%) of big sagebrush was only 6% (12 out of 215 quadrats; **Supplementary Figure 1.9**). This declined to 0% in 2012 after the 2011 fire and remained so through the duration of the study except that big sagebrush was encountered in 1 quadrat in 2014 (**Supplementary Figure 1.9**). Other shrubs were also removed entirely by fire, including gray rabbitbrush (2% in 2011 and 0% thereafter). The fire-resprouting sub-shrub broom snakeweed (*Gutierrezia sarothrae*) was the only woody species to persist on the landscape after fire, declining in 2012 but remaining rare throughout the study period (**Supplementary Figure 1.9**). Forbs were rare throughout the study and did not show response to fire. For example, locoweed (*Astragalus* spp.) and biscuitroot (*Lomatium* spp.) were the most abundant perennial forbs but did not vary in frequency of occurrence or in abundance over the seven years of study (**Supplementary Figure 1.9**).

The two perennial grasses wheatgrass and needlegrass and the two annual grasses cheatgrass and medusahead that were the focus of the study were the most frequently encountered and most abundant species throughout the study area over all 7 years of study (**Figure 3**). Cheatgrass was particularly ubiquitous, occurring in over 90% of quadrats during all years and in almost 100% of quadrats by the end of the study. Frequency of medusahead occurrence increased over the study from 34% in 2011 to 64% in 2017, with a concomitant increase in higher cover classes (**Figure 3**). All four of these species also exhibited resilience to the 2011 wildfire, maintaining or exceeding pre-burn cover by the end of the study (**Figure 3**). Notably, the two annual grasses appeared to increase over the study, in contrast with the two perennial bunchgrasses that exhibited no apparent trend. However, there was no apparent inflection in the medusahead increase following fire in 2012 as was evident for cheatgrass (**Figure 3**).

Model results for each of the grass species also revealed the apparent resilience to the 2011 fire among all four species, with strikingly low variation among ecological sites. Unconditional mean percent cover estimates, interpreted as average cover across each ecological site and year on unburned areas (burn severity = 0), for flat ground (topography and topography^2 = 0), and average water deficit conditions, showed strong effects of the fire on cheatgrass but no discernible effects on the other three species (**Figure 4**). Cheatgrass cover dropped precipitously the year after the burn but returned to pre-burn cover by 2015, 4 years after fire.

Burn severity had a strong positive influence on the model estimates of cover for the two annual grasses and a modest negative influence on cover for the perennial bunchgrasses. This influence was clear when comparing unconditional mean estimates for high burn severity (burn severity = 4; **Figure 5** vs. **Figure 4**). This increase was the result of burn severity coefficient estimates that yielded ∼300–350% increases in both occurrence and abundance of the two annual grasses for unit-level increases in burn severity (interpreting posterior means), with the strongest positive influence on medusahead. Coefficient estimates for the bunchgrasses were only slightly negative but included 0 within relatively narrow 95% credible intervals (**Figure 6**).

Topographic heterogeneity had very strong, non-linear, and contrasting influences on both the occurrence (hurdle-at-zero) and abundance (cover classes >0) model components estimated for all four grass species (**Figure 6**). When visualized as fitted lines along the topographic gradient, these influences show needlegrass occurrence strongly and needlegrass abundance modestly (due to rarity of high cover class observations for this species) associated with south facing slopes; cheatgrass abundance also associated with south-facing slopes but cheatgrass occurrence ∼100% along the entire gradient (although with increasing northward uncertainty shown in credible interval width because the few quadrats without cheatgrass occur only on north-facing slopes); medusahead associated with flat ground and shallow slopes of both aspects; and both the occurrence and abundance of wheatgrass strongly associated with north-facing slopes (**Figure 7**).

The two annual grasses were most strongly influenced by water deficit, but notably in opposite directions (**Figure 6**). Cheatgrass occurrence and abundance was negatively associated with dry high deficit years, whereas medusahead increased

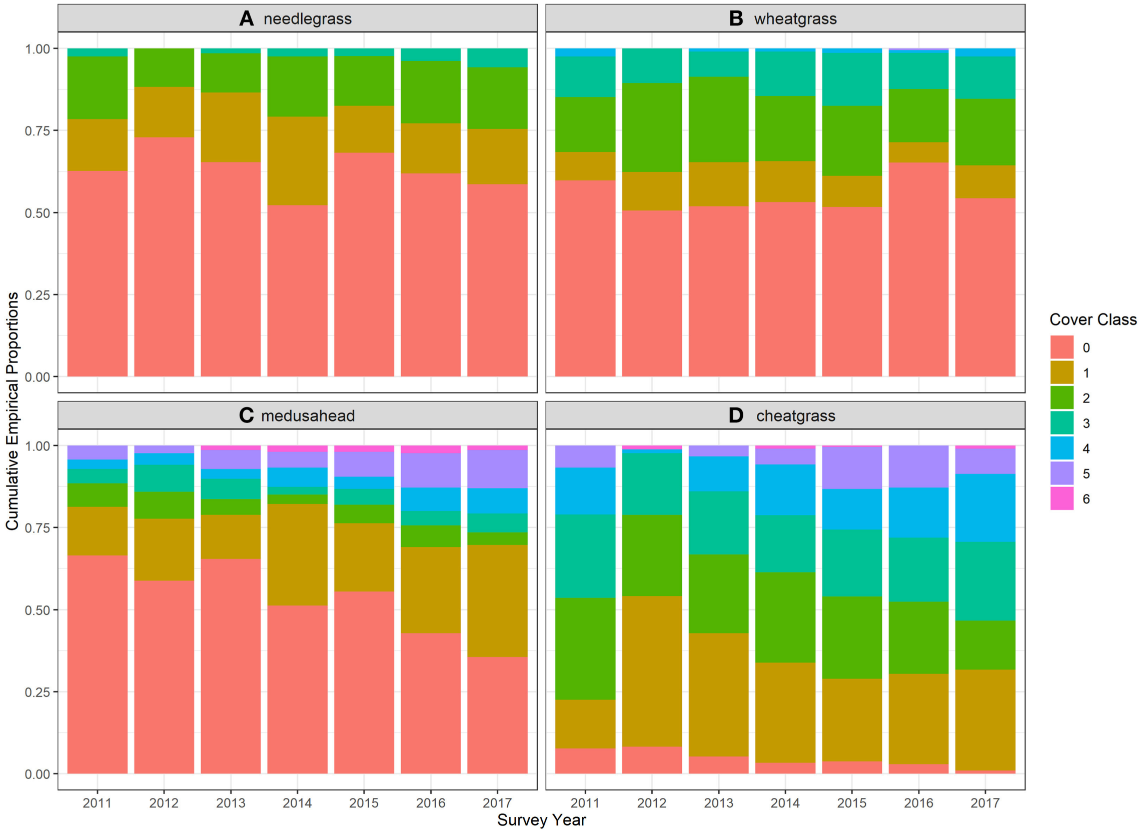

FIGURE 3 | Stacked bar charts showing the proportion of quadrats within each cover class for each year of monitoring for two native perennial bunchgrasses **(A)** Thurber's needlegrass (*Achnatherum thuberianum*) and **(B)** bluebunch wheatgrass (*Pseudoroegneria spicata*), and two non-native invasive annual grasses **(C)** medusahead (*Taeniatherum caput-medusae*) and **(D)** cheatgrass (*Bromus tectorum*).

during high deficit years. Thurber's needlegrass was also modestly associated with water deficit, reflecting a higher drought tolerance than bluebunch wheatgrass, as was also evident from the examination of topographic patterns (south-slope abundance and occurrence curves; **Figure 7**).

Predictive performance was similar among OZAB models for each species, with 64.4–88.7% of predictions within 1 cover class (needlegrass: 88.5%, medusahead: 76.5%, cheatgrass: 64.4%, and wheatgrass: 73.7%, **Supplementary Figures 1.10, 1.11, Supplementary Table 1.1**). The discrepancies between the observed cover class data (10% hold-out data set) and the predicted cover class data from all MCMC iterations (observed class-predicted class) in each model were most often 0 (**Supplementary Figure 1.10**). Patterns of predicted cover classes were similar to observed cover classes, but the OZAB models predicted less range in cover classes for all species (**Supplementary Figures 1.10, 1.11, Supplementary Table 1.1**). The first and third quantiles of the posterior distribution of Kendall's τ based on predictions from each species' model were 25.6–34.0% for needlegrass, 19.0–26.0% for medusahead, 12.2–19.8% for cheatgrass, and 27.1–32.4% for wheatgrass (**Supplementary Figures 1.10, 1.11, Supplementary Table 1.1**).

DISCUSSION

We used empirical observations and statistical models of native perennial and non-native invasive annual grass cover to evaluate the hypothesis of unidirectional fire driven state-transition to ecologically novel annual grassland in a historically grazed, repeatedly burned, and inherently low resilience/low resistance sagebrush steppe protected area. Due to historical legacies of land use and previous fires and ecological site state transition diagrams, we anticipated that the entire park unit would accelerate to an annual grass dominated state following the studied fire that occurred in 2011, but with important spatial variation among ecological sites. We found substantial evidence in favor of this hypothesis that validated the generalized state and threshold-transition dynamics understood for this aridic system but with less spatial variation among ecological sites than anticipated and with more variation along the fine-grained environmental gradients examined. Variation among gradients underscored the importance of obtaining local-scale place-based insights to implement more effective strategic management and restoration actions. The topographic position of quadrats exerted the strongest influence on variation on grass cover and apparent resilience to fire and resistance to invasion

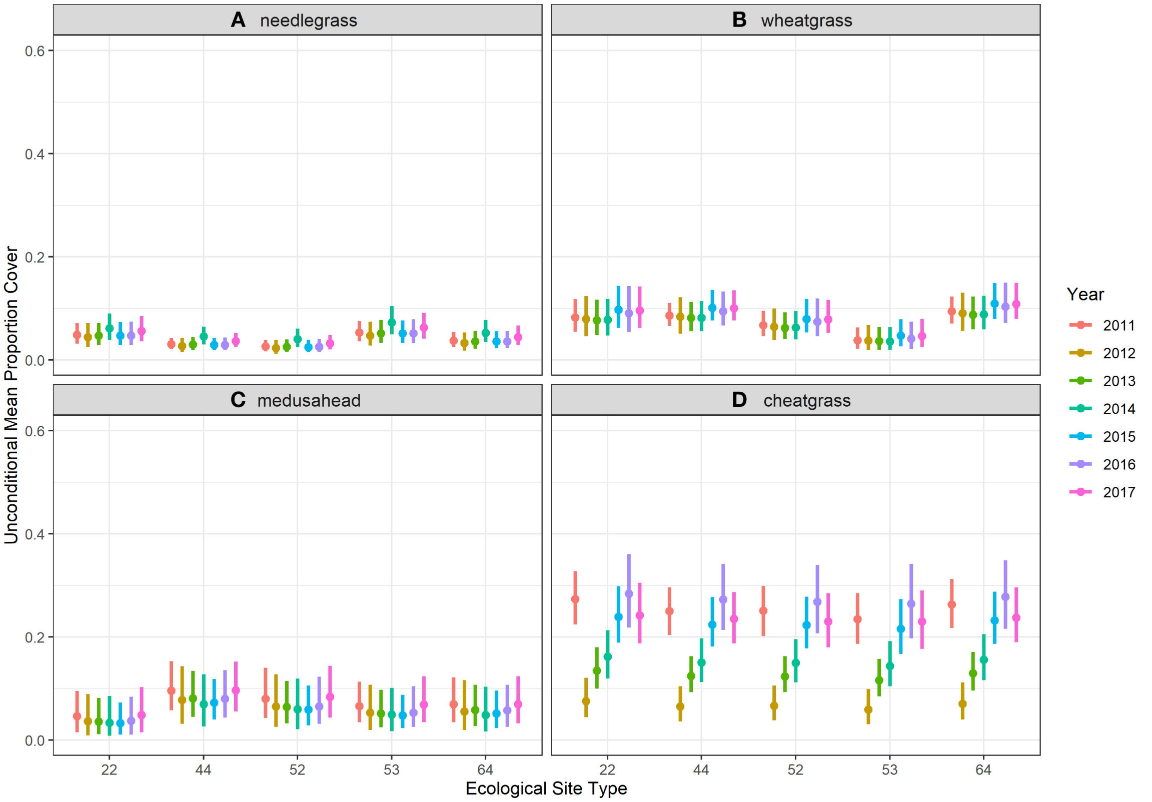

FIGURE 4 | Unconditional means estimated for each ecological site from ordinal zero-augmented beta regression models fit to ordinal cover class observations made in 1,251 (90% of the dataset for training models) quadrats surveyed during 7 years of monitoring in Clarno, John Day Fossil Beds National Monument. Estimates were plotted here for model severity factor levels set to 0 burn severity (unburned), for flat ground (topography and topography^2 = 0), and for average water deficit conditions. Ecological sites are labeled for brevity with the last two numbers of the alphanumeric code used by the Natural Resources Conservation Service (see **Table 1** for reference). **(A)** needlegrass. **(B)** wheatgrass. **(C)** medusahead. **(D)** cheatgrass.

among the two native foundational bunchgrass species examined (see photographs in **Supplementary Figure 1.8**). This insight provides a key conservation opportunity within an otherwise heavily invaded park. Steep north-facing slopes confer resilience and invasion resistance because of lower insolation and higher effective soil moisture and the Monument conservation strategy can be customized along topographic gradients (Chambers et al., 2014a, 2019; Rodhouse et al., 2014).

Variation in grass cover was minimal among the five ecological sites over time in our study. This was surprising and likely arises for three reasons. First, NRCS soil surveys are inherently imprecise for granular studies such as ours due to the logistical and financial resources available to identify and map soils and associated attributes at large scales (NRCS, 1995; Maestas et al., 2016). Because of this, there is a much higher amount of environmental heterogeneity included within mapped soil polygons than is indicated by ecological site descriptions. For example, variation in topography (slope and aspect) was as high within ecological sites as it was among ecological sites (**Supplementary Figures 1.3–1.5**). Steep, primarily north-facing slopes found in each of the ecological sites retained native perennial grasses more than on shallow slopes (**Supplementary Figure 1.8**). A second reason for low variation in grass cover among ecological sites over time in our study area was the shared attributes of soil temperature and moisture regime across all sites and only subtle differences in soil texture, historical and degraded plant community composition, and other site attributes described by NRCS for the ecological sites in the study area. Similarly, a third reason for low variation among ecological sites was the homogenizing effect (*sensu* Foster et al., 2013) of the 2011 fire, with likely cumulative influences from past fires and grazing (Chambers and Wisdom, 2009; Davies et al., 2012; Bernards and Morris, 2016; Mahood and Balch, 2019; Wood et al., 2019; Ellsworth et al., 2020). This homogenization has occurred throughout the study area across ecological sites, as community composition of all ecological sites converged toward an annual grass state. The practical implications of this outcome are that ecological site descriptions provide important general information to guide expectations and conservation actions but are limited by scale and precision, particularly for small protected areas with narrow elevational gradients and with long-lasting legacies of past land use and disturbance histories. Homogenization across ecological sites within protected areas from repeated and widespread disturbances is particularly significant because it further reduces site resilience, including spatial resilience (*sensu* Chambers et al., 2019), and site invasion resistance as fewer contiguous stands of perennial vegetation remain after each successive disturbance event.

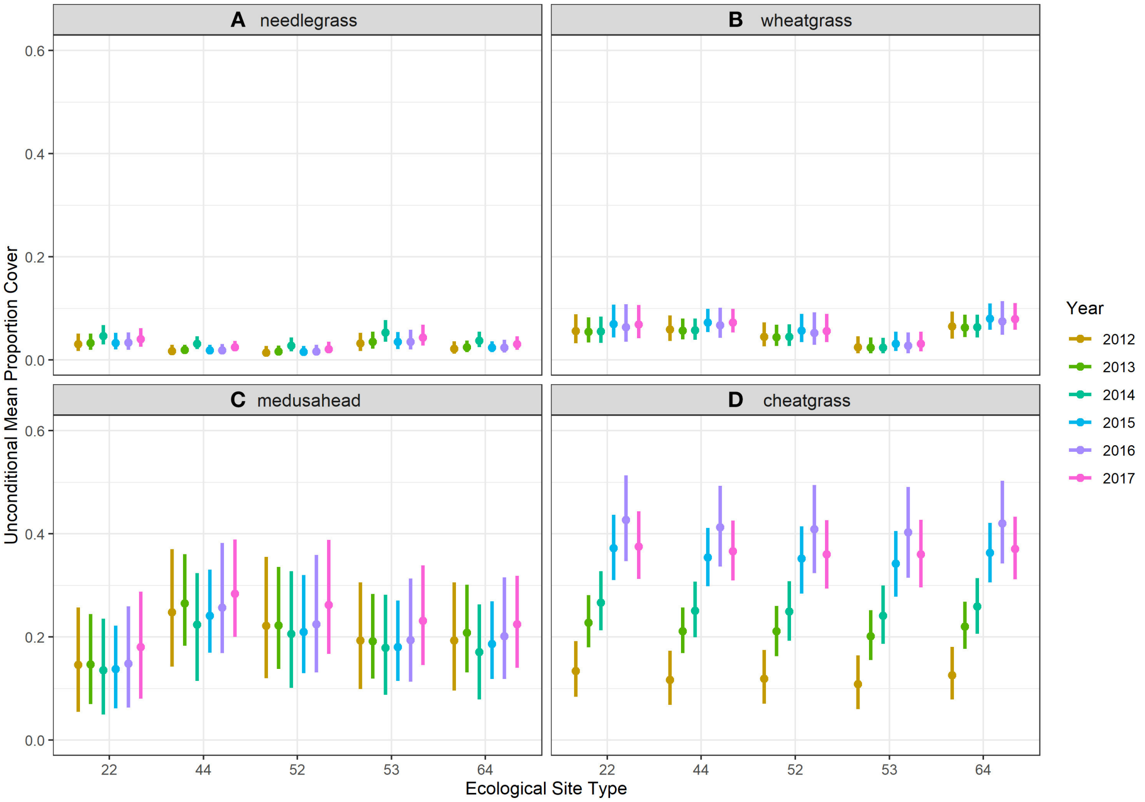

FIGURE 5 | Unconditional means estimated with ordinal zero-augmented beta regression models fit to ordinal cover class observations made in 1,251 (90% of the dataset for training models) quadrats surveyed during seven years of monitoring in Clarno, John Day Fossil Beds National Monument for each ecological site when model burn severity factor level was set to high (factor level 4). **(A)** needlegrass. **(B)** wheatgrass. **(C)** medusahead. **(D)** cheatgrass.

We observed a substantial increase in the two invasive annual grasses over time following fire, and no apparent response to fire by the two native perennial bunchgrasses, confirming the anticipated fire resiliency of all four of these species summarized by Miller et al. (2013) and previously demonstrated for the perennial bunchgrasses within our study area by Reed-Dustin et al. (2016) and Ellsworth et al. (2020). However, the two annuals also increased with burn severity, most notably medusahead. The ubiquity of cheatgrass across the study area created a ceiling to the occurrence model component (hurdle-at-zero), visualized in **Figures 3**, **7**, such that the cheatgrass fire response resulted in an initial reduction in abundance (cover) immediately following fire and a rapid recovery to pre-burn abundance. In contrast, medusahead apparently was able to invade new, severely burned areas quickly (even during the first year after fire in 2012) and did not exhibit any apparent reduction in post-burn cover such that overall trend did not reflect a short-term reduction after fire as did cheatgrass. This contrast in response between the two annual grasses is striking, especially when the differences in response to water deficit are also considered.

Medusahead exhibited a positive association with mean water deficit during October-May prior to each survey, whereas cheatgrass exhibited a negative association with deficit. This finding is consistent with the different life-history traits of the two species. Cheatgrass depends more on early-season germination in late fall and during mild winter conditions and exhibits early senescence during dry spring conditions (Bradford and Lauenroth, 2006; Chambers et al., 2007; Mangla et al., 2011). Medusahead can withstand higher water deficit during this period in part because of later germination, moisture-retaining thatch build-up from previous growing seasons, and is able to utilize late season precipitation before senescence (Mangla et al., 2011; Nafus and Davies, 2014). The accumulation of medusahead thatch reinforces a positive feedback loop of soil conditioning, favorable soil moisture, and fine fuel build-up that reduces invasion resistance and restoration (e.g., native reseeding) potential (Davies, 2008; Mangla et al., 2011; Perkins and Nowak, 2013; Nafus and Davies, 2014). The conservation implications of these medusahead characteristics are notable, suggesting that medusahead has considerable invasibility in the kinds of settings represented by our study area, can withstand drought and fire, and can quickly invade severely burned areas before native perennial grasses and shrubs can recover (Nafus and Davies, 2014). The role of cheatgrass in exacerbating the fire cycle in sagebrush steppe is well-documented but much less so for medusahead (Miller et al., 2013), and our study insights for this species contribute to the growing understanding that this species can exhibit very different ecological dynamics than cheatgrass (Miller et al., 2013).

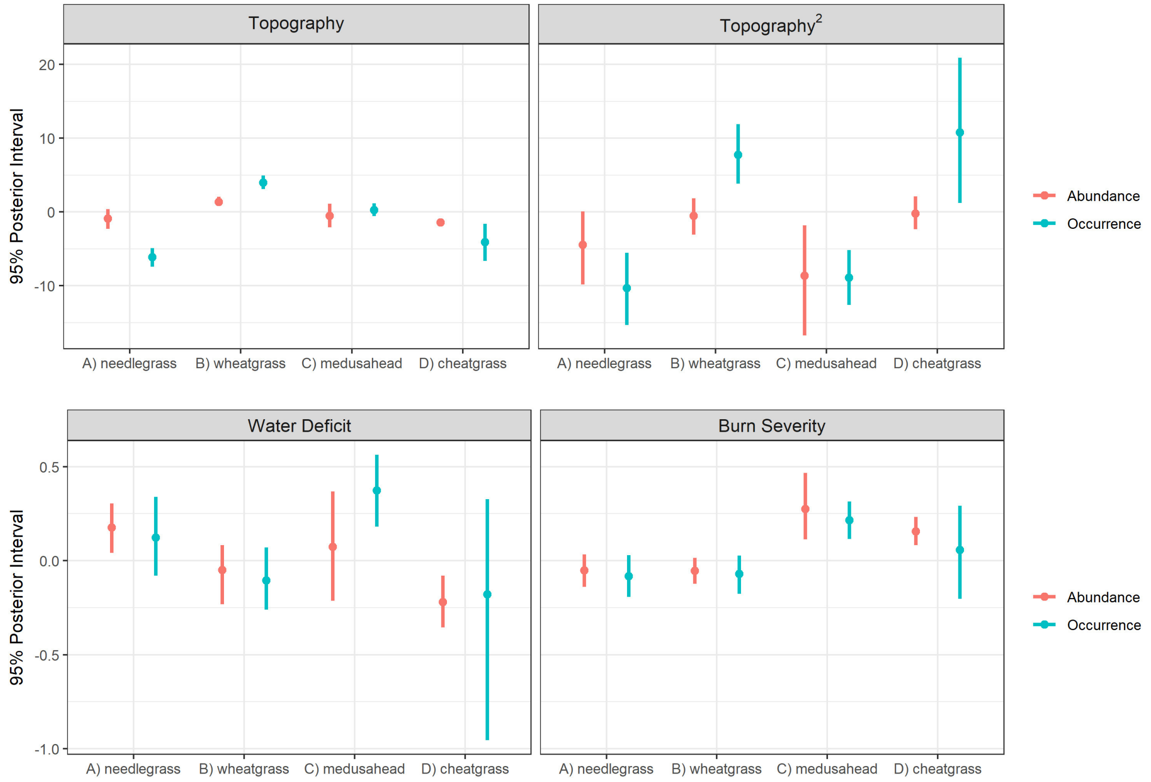

FIGURE 6 | Posterior (95%) credible intervals for the environmental covariates included in models for the four species of grasses studied in Clarno, John Day Fossil Beds National Monument. The difference in scales of y-axes demonstrates the very strong influence of topographic heterogeneity on all four grass species.

In general, our study results exemplify the precarious conservation status of the John Day Fossil Beds National Monument and other similar low-elevation sagebrush steppe protected areas. At least two species of non-native invasive annual grasses, cheatgrass, and medusahead, and increasingly a third species, wiregrass (Jones et al., 2018; Nicolli et al., 2020; Ventenata dubia), are highly aggressive competitors across large portions of low-elevation aridic sagebrush steppe, including steppe protected areas, that are capable of driving threshold-type state transitions to novel ecological conditions persisting vis a vis positive feedback loops (D'Antonio and Vitousek, 1992; Suding et al., 2004; Miller et al., 2013). We documented a complete removal of woody shrub cover that had begun prior to our study and was exacerbated by the 2011 fire (**Supplementary Figure 1.8**). This loss of woody overstory, the low cover of deep-rooted perennial forbs, and the extent of annual grass invasion indicates that the majority of the Clarno study area has crossed the threshold into the annual grass state (state 3, **Figure 2**), with only steep and primarily north-facing slopes retaining substantial native perennial vegetation. The ability of land managers to reverse these kinds of state transitions is low both because aridic low-resilience sagebrush ecosystems exhibit low productivity and high inertia and because the required restoration inputs are technologically challenging and expensive (e.g., James et al., 2013). Therefore, these kinds of sites are often ranked low in priority, especially within the context of sage grouse (*Centrocercus urophasianus*) habitat management (e.g., Chambers et al., 2019). However, the slopes where tall-stature perennial bunchgrasses (specifically wheatgrass and needlegrass in our study area) persist with sufficient cover (e.g., ≥25%) does create a foothold for land managers when broader conservation objectives are pursued. Despite the species-specific fire resilience of wheatgrass and needlegrass exhibited in our study and elsewhere (Miller et al., 2013; Reed-Dustin et al., 2016; Ellsworth et al., 2020; e.g., Ellsworth and Kauffman 2010), the general resilience and invasion resistance of these ecological sites are so low that protection of remaining bunchgrass slopes from fire is reinforced as a core objective that is widely recommended (e.g., Chambers et al., 2019) and already outlined in Monument conservation plans (Rodhouse et al., 2014; Hoh et al., 2015; Shinderman et al., 2020). Protection of the extant contiguous perennial bunchgrass communities on both north- and south-facing slopes would contribute to diversity of bunchgrass community types (i.e., needlegrass and wheatgrass) although bunchgrass-dominant north slopes are more abundant (e.g., **Figure 7**) and are more likely to persist. However, over time, with sufficient operational capacity, it may also be possible to restore bunchgrass slopes outward from persistent bunchgrass stands, possibly even on hotter south aspects. However, without sufficient capacity, a triage strategy will be required so that protection of remaining quasi-intact bunchgrass slopes is prioritized (Chambers and Wisdom, 2009). The largest

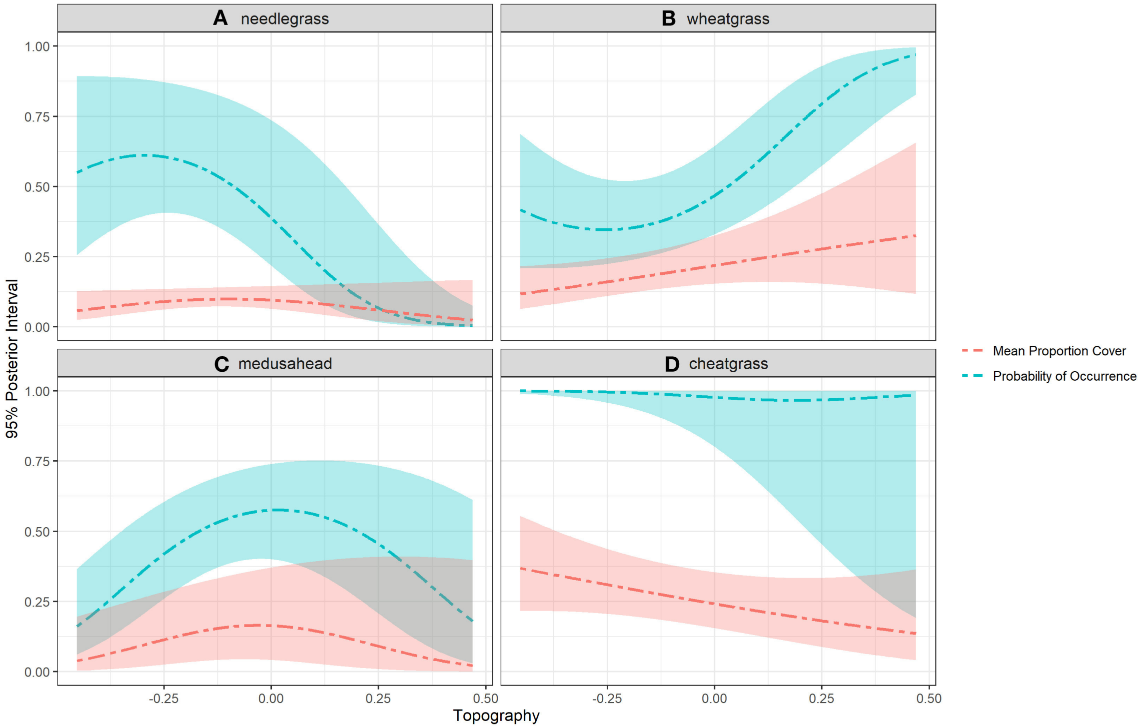

FIGURE 7 | Fitted regression curves along the topographic gradient for four grass species studied in Clarno, John Day Fossil Beds National Monument. Topography was measured as sin(slope) x cos(aspect) and included as a 2-parameter quadratic term in the model. Steep south-facing slopes trend toward −1 and steep north-facing slopes trend toward 1. **(A)** needlegrass. **(B)** wheatgrass. **(C)** medusahead. **(D)** cheatgrass.

contiguous stands should be highest priority. We suggest that our strategy of integrating empirical data with conceptual and statistical models about state transitions is an effective science-based approach that could be replicated across the protected-area network to accelerate the operational application of resilience and resistance concepts to sagebrush steppe conservation, including integration into fire management operations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

TR and KI designed the study. TR collected the data and wrote the manuscript. LB analyzed the data. KI and LB provided substantial contributions to the manuscript. All authors edited the manuscript and agreed to its content.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Agresti, A. (2010). *Analysis of Ordinal Categorical Data*. Hoboken, NJ: John Wiley and Sons. doi: 10.1002/9780470594001

Balch, J. K., Bradley, B. A., D'Antonio, C. M., and Gomez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Glob. Change Biol.* 19, 173–183. doi: 10.1111/gcb.12046

Bangert, R., and Huntly, N. (2010). The distribution of native and exotic plants in a fragmented sagebrush-steppe landscape. *Biol. Invasions* 12, 1627–1640. doi: 10.1007/s10530-009-9575-4

Bernards, S. J., and Morris, L. R. (2016). Influence of topography on long-term successional trajectories in canyon grasslands. *Appl. Vegetat. Sci.* 20, 236–246. doi: 10.1111/avsc.12272

Bradford, J. B., and Lauenroth, W. K. (2006). Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. *J. Vegetat. Sci.* 17, 693–704. doi: 10.1111/j.1654-1103.2006.tb02493.x

Bradford, J. B., Schlaepfer, D. R., Lauenroth, W. K., Palmquist, K. A., Chambers, J. C., Maestas, J. D., et al. (2019). Climate-driven shifts in soil temperature and moisture regimes suggest opportunities to enhance assessments of dryland resilience and resistance. *Front. Ecol. Evolut.* 7:358. doi: 10.3389/fevo.2019.00358

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., et al. (2004). Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688. doi: 10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Bukowski, B. E., and Baker, W. L. (2013). Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. *Ecol. Appl.* 23, 546–564. doi: 10.1890/12-0844.1

Caicco, S. L., Scott, J. M., Butterfield, B., and Csuti, B. (1995). A gap analysis of the management status of the vegetation of Idaho (U.S.A.). *Conserv. Biol.* 9, 498–511. doi: 10.1046/j.1523-1739.1995.09030498.x

Chambers, J. C., Bradley, B. A., Brown, C. S., D'Antonio, C. D., Germino, M. J., Grace, J. B., et al. (2014a). Resilience to stress and disturbance and resistance to *Bromus tectorum L. invasion* in cold desert shrublands of western North America. *Ecosystems* 17, 360–375. doi: 10.1007/s10021-013-9725-5

Chambers, J. C., Brooks, M. L., Germino, M. J., Maestas, J. D., Board, D. I., Jones, M. O., et al. (2019). Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. *Front. Ecol. Evolut.* 7:185. doi: 10.3389/fevo.2019.00185

Chambers, J. C., Miller, R. F., Board, D. I., Pyke, D. A., Roundy, B. A., Grace, J. B., et al. (2014c). Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatements. *Rangel. Ecol. Manage.* 67, 440–454. doi: 10.2111/REM-D-13-00074.1

Chambers, J. C., Pyke, D. A., Maestas, J. D., Pellant, M., Boyd, C. S., Campbell, S. B., et al. (2014b). *Using Resistance and Resilience Concepts to Reduce Impacts of Invasive Annual Grasses and Altered Fire Regimes on the Sagebrush Ecosystem and Greater Sage-Grouse: A Strategic Multi-Scale Approach. Gen. Tech. Rep. RMRS-GTR-326*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. doi: 10.2737/RMRS-GTR-326

Chambers, J. C., Roundy, B. A., Blank, R. R., Meyer, S. E., and Whittaker, A. (2007). What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecol. Monogr.* 77, 117–145. doi: 10.1890/05-1991

Chambers, J. C., and Wisdom, M. J. (2009). Priority research and management issues for the imperiled Great Basin of the western United States. *Restor. Ecol.* 17, 707–714. doi: 10.1111/j.1526-100X.2009.00588.x

Damgaard, C. F., and Irvine, K. M. (2019). Using the beta distribution to analyse plant cover data. *J. Ecol.* 107, 2747–2759. doi: 10.1111/1365-2745.13200

D'Antonio, C. M., and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87. doi: 10.1146/annurev.es.23.110192.000431

Daubenmire, R. F. (1959). A canopy-coverage method. *Northwest Sci.* 33:43–64.

Davies, G. M., Bakker, J. D., Dettweiler-Robinson, E., Dunwiddie, P. W., Hall, S. A., Downs, J., et al. (2012). Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecol Appl.* 22, 1562–1577. doi: 10.1890/10-2089.1

Davies, K. W. (2008). Medusahead dispersal and establishment in sagebrush steppe plant communities. *Rangel. Ecol. Manage.* 61, 110–115. doi: 10.2111/07-041R2.1

Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., Svejcar, T. J., and Gregg, M. A. (2011). Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biol. Conserv.* 144, 2573–2584. doi: 10.1016/j.biocon.2011.07.016

Dilts, T. E., Weisberg, P. J., Dencker, C. M., and Chambers, J. C. (2015). Functionally relevant climate variables for arid lands: a climatic water deficit approach for modelling desert shrub distributions. *J. Biogeogr.* 42, 1986–1997. doi: 10.1111/jbi.12561

Ellsworth, L. M., and Kauffman, J. B. (2010). Native bunchgrass response to prescribed fire in ungrazed mountain big sagebrush ecosystems. *Fire Ecol.* 6, 86–96. doi: 10.4996/fireecology.0603086

Ellsworth, L. M., Kauffman, J. B., Reis, S. A., Sapsis, D., and Moseley, K. (2020). Repeated fire altered succession and increased fire behavior in basin big sagebrush-native perennial grasslands. *Ecosphere* 11:e03124. doi: 10.1002/ecs2.3124

Erixson, J. A., Cogan, D., and Von Loh, J. (2011). *Vegetation Inventory Project: John Day Fossil Beds National Monument. Natural Resource Technical Report NPS/UCBN/NRTR-2011/419*. Fort Collins, CO: National Park Service.

Esposito, D. M., Rodhouse, T. J., Mata-Gonzalez, R., and Hovland, M. (2019). Differential species responses to aspects of resistance to invasion in two Columbia Plateau protected areas. *Rangel. Ecol. Manag.* 72, 773–782. doi: 10.1016/j.rama.2019.05.006

Fancy, S. G., Gross, J. E., and Carter, S. L. (2009). Monitoring the condition of natural resources in US national parks. *Environ. Monit. Assess.* 151, 161–174. doi: 10.1007/s10661-008-0257-y

Ferrari, S. L. P., and Cribari-Neto, F. (2004). Beta regression for modelling rates and proportions. *J. Appl. Stat.* 31, 799–815. doi: 10.1080/0266476042000214501

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., et al. (2013). The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88. doi: 10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2

Gelman, A., and Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. New York, NY: Cambridge University Press. doi: 10.1017/CBO9780511790942

Hoh, S., Rodhouse, T. J., Esposito, D., Sheley, R., and Smith, B. (2015). *A Framework for Ecologically-Based Invasive Plant Management: John Day Fossil Beds National Monument. Natural Resource Report NPS/UCBN/NRR-2015/911*. Fort Collins, CO: National Park Service.

Irvine, K. M., and Rodhouse, T. J. (2010). Power analysis for trend in ordinal cover classes: implications for long-term vegetation monitoring. *J. Veget. Sci.* 21, 1152–1161. doi: 10.1111/j.1654-1103.2010.01214.x

Irvine, K. M., Rodhouse, T. J., and Keren, I. N. (2016). Extending ordinal regression with a latent zero-augmented beta distribution. *J. Agric. Biol. Environ. Stat.* 21, 619–640. doi: 10.1007/s13253-016-0265-2

Irvine, K. M., Wright, W. J., Shanahan, E. K., and Rodhouse, T. J. (2019). Cohesive framework for modelling plant cover class data. *Methods Ecol. Evol.* 10, 1749–1760. doi: 10.1111/2041-210X.13262

James, J. J., Sheley, R. L., Erickson, T., Rollins, K. S., Taylor, M. H., and Dixon, K. W. (2013). A systems approach to restoring degraded drylands. *J. Appl. Ecol.* 50, 730–739. doi: 10.1111/1365-2664.12090

Jones, L. C., Norton, N., and Prather, T. S. (2018). Indicators of ventenata (*Ventenata dubia*) invasion in sagebrush steppe rangelands. *Invasive Plant. Sci. Manag.* 11, 1–9. doi: 10.1017/inp.2018.7

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. *Int. J. Wildland Fire* 18, 116–126. doi: 10.1071/WF07049

Key, C. H., and Benson, N. C. (2006). "Landscape assessment: ground measure of severity, the composite burn index, and remote sensing of severity, the normalized burn index," in *FIREMON: Fire effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR164-CD: LA1-51Lutes*. eds, D. C. Keane, R. E. Caratti, J. F. Key, C. H. Benson, N. C. Sutherland, S., and L. J. Gangi (Ogden, UT).

Kincaid, T. M., and Olsen, A. R. (2019). *spsurvey: Spatial Survey Design and Analysis. R package version* 4.0. Available online at: https://cran.r-project.org/web/packages/spsurvey/index.html (accessed November 11, 2020).

Lutz, J. A., van Wagtendonk, J. W., and Franklin, J. F. (2010). Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *J. Biogeogr.* 37, 936–950. doi: 10.1111/j.1365-2699.2009.02268.x

MacDonald, T. L. (2003). Review of environmental monitoring methods: survey designs. *Environ. Monit. Assess.* 85, 277–292. doi: 10.1023/A:1023954311636

Maestas, J. D., Campbell, S. B., Chambers, J. C., Pellant, M., and Miller, R. F. (2016). Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. *Rangelands* 38, 120–128. doi: 10.1016/j.rala.2016.02.002

Mahood, A. L., and Balch, J. K. (2019). Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984-2014). *Ecosphere* 10:e02591. doi: 10.1002/ecs2.2591

Mangla, S., Sheley, R. L., and James, J. J. (2011). Field growth comparisons of invasive alien annual and native perennial grasses in monocultures. *J. Arid. Environ.* 75, 206–210. doi: 10.1016/j.jaridenv.2010.09.015

Masek, J. G., Vermote, E. F., Saleous, N., Wolfe, R., Hall, F. G., Huemmrich, F., et al. (2006). A Landsat surface reflectance data set for North America, 1990-100. *IEEE Geosci. Remote Sens. Lett.* 3, 68–72. doi: 10.1109/LGRS.2005.857030

McCune, B., and Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *J. Veget. Sci.* 13, 603–606. doi: 10.1111/j.1654-1103.2002.tb02087.x

Miller, R. F., Chambers, J. C., Pyke, D. A., Pierson, F. B., and Williams, J. C. (2013). *A Review of Fire Effects on Vegetation and Soils in the Great Basin region: Response and Ecological Site Characteristics. Gen. Tech Rep. RMRS-GTR-308*. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. doi: 10.2737/RMRS-GTR-308

Nafus, A. M., and Davies, K. W. (2014). Medusahead ecology and management: California annual grasslands to the intermountain west. *Invasive Plant. Sci. Manag.* 7, 210–221. doi: 10.1614/IPSM-D-13-00077.1

Nicolli, M., Rodhouse, T. J., Stucki, D. S., and Shinderman, M. (2020). Rapid invasion by the annual grass *Ventenata dubia* into protected-area low-elevation sagebrush steppe. *Western N. Am. Natural.* 80, 243–252. doi: 10.3398/064.080.0212

Noss, R. F., LaRoe, E. T. III, and Scott, J. M. (1995). *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28*. Washington, DC: National Biological Service.

NPS. (2012). *National Park Service-SRI-Soil Survey Geographic (SSURGO) for National Park Service Units. National Park Service Inventory and Monitoring Program*. Available online at: https://irma.nps.gov/DataStore/Reference/Profile/2190427 (accessed November 11, 2020).

NRCS. (1995). *Soil Survey Geographic (SSURGO) Data Base: Data Use Information*. US Department of Agriculture Natural Resources Conservation Service, National Soil Survey.

Perkins, L. B., and Nowak, R. S. (2013). Native and non-native grasses generate common types of plant-soil feedbacks by altering soil nutrients and microbial communities. *Oikos* 122, 199–208. doi: 10.1111/j.1600-0706.2012.20592.x

Plummer, M. (2003). "JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling," in *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*. eds, K. Hornik, F. Leisch, and A. Zeileis (Vienn). Available online at: http://www.ci.tuwien.ac.at/Conferences/DSC-2003/

Plummer, M. (2019). rjags: Bayesian graphical models using MCMC. R package version 4.9. Available online at: https://CRAN.R-project.org/package=rjags

Powell, S. L., Hansen, A. J., Rodhouse, T. J., Garrett, L. K., Betancourt, J. L., Dicus, G. H., et al. (2013). Woodland dynamics at the northern range periphery: a challenge for protected area management in a changing world. *PLoS ONE* 8:e70454. doi: 10.1371/journal.pone.0070454

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.R-project.org/ (accessed November 11, 2020).

Reed-Dustin, C. M., Mata-Gonzalez, R., and Rodhouse, T. J. (2016). Long-term fire effects on native and invasive grasses in protected area sagebrush steppe. *Rangel. Ecol. Manag.* 69, 257–264. doi: 10.1016/j.rama.2016.03.001

Rodhouse, T. J., Irvine, K. M., Sheley, R. L., Smith, B., Hoh, S., Esposito, D., et al. (2014). Predicting foundation bunchgrass species abundances: model-assisted decision-making in protected-area sagebrush steppe. *Ecosphere* 5:108. doi: 10.1890/ES14-00169.1

Shinderman, M., Hovland, M., Oedekerk, C., Lamet, A. J., and Rodhouse, T. J. (2020). *Managing for Resilience to Fire and Resistance to Annual Grass Invasion in Upland Sagebrush Steppe: John Day Fossil Beds National Monument. Natural Resource Report NPS/UCBN/NRR-2020/2144*. Fort Collins, CO: National Park Service.

Stage, A. R. (1976). An expression for the effect of aspect, slope, and habitat type on tree growth. *Forest Sci.* 4, 457–460.

Stephenson, N. L. (1990). Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.* 135, 649–670. doi: 10.1086/285067

Stephenson, N. L. (1998). Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* 25, 855–870. doi: 10.1046/j.1365-2699.1998.00233.x

Stevens, D. L., and Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *J. Am. Stat. Assoc.* 99, 262–278. doi: 10.1198/016214504000000250

Stoms, D. M., Davis, F. W., Driese, K. L., Cassidy, K. M., and Murray, M. P. (1998). Gap analysis of the vegetation of the intermountain semi-desert ecoregion. *Great Basin Natural.* 58, 199–216.

Stringham, T. K., Krueger, W. C., and Shaver, P. L. (2003). State and transition modeling: an ecological process approach. *J. Range Manag.* 56, 106–113. doi: 10.2307/4003893

Suding, K. N., Gross, K. L., and Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53. doi: 10.1016/j.tree.2003.10.005

Thoma, D. P., Munson, S. M., Irvine, K. M., Witwicki, D. L., and Bunting, E. L. (2016). Semi-arid vegetation response to antecedent climate and water balance windows. *Appl. Veget. Sci.* 3, 413–429. doi: 10.1111/avsc.12232

Thoma, D. P., Tercek, M. T., Schweiger, E. W., Munson, S. M., Gross, J. E., and Olliff, S. T. (2020). Water balance as an indicator of natural resource condition: case studies from Great Sand Dunes National Park and Preserve. *Glob. Ecol. Conserv.* 24:e01300. doi: 10.1016/j.gecco.2020.e01300

Thornthwaite, C. W., and Mather, J. R. (1955). The water balance. *Publications Climatol.* 8, 1–104.

Thornton, P. E., Thornton, M. M., Mayer, B. W., Wei, Y., Devarakonda, R., Vose, R. S., et al. (2018). *Daymet: Daily Surface Weather Data on a 1-km Grid for North America, version 3*. Oakridge, TN.

Urquhart, N. S., and Kincaid, T. M. (1999). Designs for detecting trend from repeated surveys of ecological resources. *J. Agric. Biol. Environ. Stat.* 4, 404–414. doi: 10.2307/1400498

Wood, D. J. A., Seipel, T., Irvine, K. M., Rew, L. J., and Stoy, P. C. (2019). Fire and development influences on sagebrush community plant groups across a climate gradient in northern Nevada. *Ecosphere* 10:e02990. doi: 10.1002/ecs2.2990

Yeo, J. J., Rodhouse, T. J., Dicus, G. H., Irvine, K. M., and Garrett, L. K. (2009). *Upper Columbia Basin Network Sagebrush Steppe Vegetation Monitoring Protocol: Narrative version 1.0. Natural Resource Report NPS/UCBN/NRR-2009/142*. Fort Collins, CO: National Park Service.

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Contrasting Geographic Patterns of Ignition Probability and Burn Severity in the Mojave Desert

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The extent and frequency of fire has increased in many arid systems over the last century, with a large proportion of area in some regions undergoing transitions to novel conditions. Portions of the Mojave Desert in southwestern North America have undergone such transitions, most often from woody to herbaceous-dominated systems. These transitions have often been attributed to the proliferation of invasive annual grasses that promote more frequent fire, but recent evidence indicates that transitions can also occur independent of fire frequency if burn severity is high. In addition, high probability of ignition (i.e., potentially high fire frequency) and high burn severity may not always be geographically related. Therefore, our goals were to: (1) map potential burn severity, fire frequency, and probability of ignition across the Mojave; and, (2) evaluate spatial association among predicted burn severity, fire frequency and probability of ignition. We first mapped perimeters of 250 wildfires > 405 ha that occurred from 1972 to 2010, then extracted data on fire frequency (number of times burned from 1972 to 2010), burn severity (the difference Normalized Burn Ratio), and 15 predictor variables representing physiography, climate, ignition, and vegetation. Maximum entropy was used to predict probability of ignition and Random Forest models were used to predict dNBR and fire frequency. Areas with high burn severity and high ignition probability had opposite spatial trends; areas with high burn severity were predicted to predominantly be in the northwest part of the region whereas areas with high ignition probability were predicted to be in the northeast. The models indicate the existence of a number of spatially structured but temporally dynamic fire regimes throughout the Mojave Desert. Two prevalent and ecologically significant regimes include one with frequent fires of low to moderate severity and another with infrequent fire of high severity. Areas with high fire frequency are currently limited in extent (<1% total area). However, cover of invasive grasses can remain high decades after a burn of high or moderate severity, so grass-fire cycles could develop in areas where there may be expectations of infrequent fire as well as those with relatively high fire frequency.

Keywords: fire regimes, gradients, heterogeneity, invasive species, grass-fire cycle, machine learning, point process models, spatial dynamics

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INTRODUCTION

Fire in the North American deserts was historically characterized as a regime of relatively small, infrequent, and patchy burns (Wright and Bailey, 1982). This perspective has gradually evolved with increasing recognition that it applied mainly to lower elevations where productivity is low and vegetation discontinuous (Brooks et al., 2018). Moreover, an interplay between elevation, latitude and topography results in significant climatic variation both among and within the four major North American deserts (Great Basin, Mojave, Sonoran, and Chihuahuan; MacMahon and Wagner, 1985; Hereford et al., 2006; Brooks and Chambers, 2011). These physiographic-climatic interactions potentially result in not just one but multiple fire regimes both within and among the desert regions of North America (Tagestad et al., 2016; Brooks et al., 2018; Chambers et al., 2019).

Interest in fire in the North American deserts has been increasing (Brooks and Pyke, 2001; Abatzoglou and Kolden, 2011, Brooks and Chambers, 2011), but appreciation of how variation in vegetation, topography, and climate shapes desert fire regimes has been slow to take hold. There have been a number of recent studies on wildfire activity in the western United States, especially in forests and shrublands (Collins et al., 2006; Westerling et al., 2006; Littell et al., 2009; Miller et al., 2012; Abatzoglou and Kolden, 2013; Dennison et al., 2014). Deserts were integrated into some of these studies, but the criteria used to delimit them differed considerably among the studies. In some the boundaries were based on administrative or management borders, while others pooled or split the deserts irrespective of fundamentally different ecological characteristics. Thus, from a bioregional perspective, the delineations made little ecological sense. Moreover, not accounting for the extensive physiognomic heterogeneity among and within the deserts implied they were represented by one fire regime. As a result, while the studies reported an increase in numbers of fires and area burned in the western United States, inferring that those trends are representative of the deserts is problematic. This becomes especially apparent when studies that were focused on a specific desert report patterns markedly different from the patterns reported in the large-scale studies (Brooks and Matchett, 2006; Syphard et al., 2017; Klinger et al. unpublished).

Despite these problems, it would be inappropriate to think that the factors generally regarded as being responsible for increased fire activity in forests and shrublands do not also influence fire regimes in the deserts. These include shifts in climate (Westerling et al., 2003; Littell et al., 2009), the buildup of woody vegetation (often because of historic fire suppression by humans), and promotion of high ignition rates by invasive annual grasses (D'Antonio and Vitousek, 1992; Brooks et al., 2004). These factors rarely act in isolation though. Rather, their interactions are the critical elements of both fire activity and dynamics in post-fire vegetation (Abatzoglou and Kolden, 2013; Overpeck, 2013). Moreover, both the magnitude and direction of their interactions can be modified by the complex physiography of the deserts (Klinger and Brooks, 2017).

The amount and seasonality of precipitation are recognized as the most important large-scale drivers of fire in the deserts (Brooks and Chambers, 2011; Tagestad et al., 2016). Precipitation is influenced greatly by elevation, latitude and longitude, so rainfall patterns among and within the deserts have high heterogeneity (MacMahon and Wagner, 1985; Hereford et al., 2006). Because vegetation biomass is strongly related to precipitation in arid ecosystems it varies greatly along gradients of elevation and latitude (Chambers et al., 2019). This results in fire activity potentially being limited by fuel at lower elevations and latitudes and by ignition at higher elevations and latitudes (Brooks and Matchett, 2006). The interplay between fuel and ignition can be altered by invasive annual grasses though. They produce a fuel layer that is continuous and easily ignited, which can lead to more frequent ignitions as well as communities where they are the dominant species (Brooks and Pyke, 2001). In some instances impacts from invasive annual grasses can be localized and diminish over time (Klinger and Brooks, 2017), but in others they can result in the transformation of entire ecosystems (Brooks et al., 2004; Zouhar et al., 2008).

The grass-fire cycle (GFC) is a conceptual representation of the positive feedback between fire regimes and post-fire vegetation communities (D'Antonio and Vitousek, 1992; Brooks et al., 2004). Most research has focused on how the GFC increases fire frequency (i.e., shortens fire return intervals), resulting over time in conversion of woody-dominated communities to invasive grass-dominated communities. Frequency is only one component of a fire regime though. A recent chronosequence study throughout the Mojave Desert (Mojave from hereon) reported long-term (30–40 years) conversions occurred following single fires that were of moderate to high burn severity (Klinger and Brooks, 2017). High fire frequency also resulted in long-term shifts in herbaceous communities independent of burn severity, indicating the existence of two pathways for fire-driven transformation of vegetation communities (Klinger and Brooks, 2017).

The GFC has been reported to occur in the Mojave for more than 20 years (Brooks, 1999; Brooks and Esque, 2002; Brooks and Matchett, 2006). A large portion of the region has suitable habitat for several invasive grass species (Underwood et al., 2019) and fire frequency tends to be high where habitat for invasive annual grass species is suitable (Balch et al., 2013; Underwood et al., 2019). This suggests the GFC could potentially occur throughout a very large portion of the Mojave (Brooks and Matchett, 2006; Klinger and Brooks, 2017; Fusco et al., 2019; Underwood et al., 2019). However, its occurrence has only been substantiated in specific elevation zones and regions (Brooks et al., 2018).

Theoretically, a combination of high burn severity and high fire frequency would have the highest expectation for establishment of a GFC. This is likely to be very uncommon though, because heavy woody fuel is sparse when an area burns repeatedly in a relatively short period of time (Steel et al., 2015). In a region such as the Mojave, where physiography and climate have such high heterogeneity (Tagestad et al., 2016; Klinger et al., 2019), there is potential for spatial structuring in both fire regimes and post-fire vegetation communities (Brooks et al., 2018). In some parts of the region fire could be a relatively frequent event but of low to moderate severity, resulting in largely herbaceous post-fire plant communities dominated by invasive annual grass. In other parts fire could be considerably less frequent, but when it did occur a large portion of the area that burned would likely be of high or very high severity. These high severity sites would be predisposed to greater establishment of invasive annual grass, and whether they underwent long-term conversion or not would depend on distribution and abundance of invasive annual grasses in the area (Brooks and Berry, 2006; Underwood et al., 2019). If sites did become dominated by invasive annual grasses, the possibility of a GFC developing would increase greatly.

Prior studies of spatio-temporal patterns of fire in the Mojave either focused on the number of fires and area burned (Brooks and Matchett, 2006; Tagestad et al., 2016) or were restricted in spatial and/or temporal extent (Hegeman et al., 2014). Therefore, we undertook this study to address five main questions:

(1) How did fire frequency and burn severity interact to shape fire regimes across the Mojave along gradients of latitude, longitude, and elevation?
(2) What were the predicted spatial patterns of probability of ignition fire frequency, and burn severity across the Mojave along gradients of latitude, longitude, and elevation?
(3) What were the most important climate, physiographic, and vegetation variables related to predicted patterns of ignition, fire frequency and burn severity?
(4) What was the spatial association between predicted probability of ignition and burn severity?
(5) How extensive was the grass-fire cycle in the Mojave and where was it most likely to occur?

Our objectives were to: (1) map and evaluate the spatial patterns of large (>405 ha) wildfires across the Mojave from 1972 through 2010, especially in regard to fire frequency; (2) model the probability of ignition, fire frequency, and level of burn severity across the Mojave and evaluate the contribution of variables related to climate, physiography, and vegetation to the models; and, (3) evaluate spatial relationships among probability of ignition, fire frequency and burn severity to identify what fire regimes occurred in the Mojave and where those driven predominantly by fire frequency occurred and where those driven predominantly by burn severity occurred.

MATERIALS AND METHODS

The Mojave Desert

The Mojave is the smallest of the four major North American deserts (≈152,000 km^2) and considered transitional in climate between the colder Great Basin Desert to the north and the warmer Sonoran Desert to the south/southeast. Winter temperatures range from −20°C at higher elevations to −5°C at lower elevations, while summer temperatures range from 30°C (high elevation) to 50°C (low elevation). It is the driest of the four major North American deserts, but there is substantial geographic variability in precipitation patterns (Hereford et al., 2006; Tagestad et al., 2016). The total annual amount tends to be greater at higher latitudes and elevations, while the proportion occurring in the summer monsoon season is generally greater in the eastern and southeastern parts of the region (≈24% to 29% vs. 13% to 18% in more westerly areas). This strong variability in precipitation, as well as temperature, topography, and vegetation, has led to the designation of six subregions within the Mojave (**Figure 1**; Webb et al., 2009).

The Mojave is bounded by the Sierra Nevada range to the west, the Colorado Plateau to the east, and the San Bernardino, San Gabriel, and Tehachapi ranges along its southwestern margins. Dozens of small mountain ranges are interspersed throughout the region, resulting in complex topography where elevations range from -85 m to 3,633 m. The mountain ranges bordering the Mojave create a rain shadow effect on west/northwest originating winter storms and are a major reason why the region is so arid. Monsoon season (July–September) precipitation results largely from the influence of the Colorado Plateau and the interior mountain ranges on moist southerly airflows. This pattern creates localized thunderstorms with numerous lightning strikes, which are the main source of ignition for the majority of large fires in the region (Brooks and Matchett, 2006; Tagestad et al., 2016; Brooks et al., 2018).

Vegetation in the Mojave is assembled primarily along an elevation gradient, although soils contribute to structure and composition as well (Brooks et al., 2018; Klinger et al., 2019). Native-dominated communities in the lower elevations (≈<1,200 m) are comprised primarily of sparse shrub cover (≈7–10%) of low stature (0.5–1.5 m). Native-dominated communities in the mid-elevations (≈1,200–1,800 m) are also dominated by shrubs, but cover is generally greater (≈15–20%) and stature of the shrubs tends to be higher (1–2 m) than in the lower elevations. Higher elevation communities are a mix of shrubs and trees [e.g., junipers (*Juniperus* spp.) and pines (*Pinus* spp.)]; woody cover typically ranges from ≈25–40%. Native forb and perennial grass species are common in all communities along the elevation gradient. Their cover is generally low (<≈3%), but during wet years it can increase 10–20×.

There are few widespread non-native species in the Mojave Desert (Abella, 2010), although cover of three annual grass [Mediterranean split grass (*Schismus barbatus* and *Schismus Arabicus*), red brome (*Bromus rubens*), cheatgrass (*Bromus tectorum*)] and one annual forb species [red-stemmed filaree (*Erodium cicutarium*)] can be high in burned areas, especially in the initial 5–10 years after fire (Brooks, 1999; Klinger and Brooks, 2017; Underwood et al., 2019). The three grasses are generally considered to be transformer species (Richardson et al., 2000) in the North American deserts because they can alter fire regimes and dominate post-fire communities (Brooks, 1999; Chambers et al., 2007; Bradley et al., 2018). In the Mojave these grasses sort along an elevation gradient, with split-grass being most abundant at lower elevations, red brome in mid-elevations, and cheatgrass in upper elevations (Underwood et al., 2019). The distribution of red-stemmed filaree is similar to that of red brome, but while it can dominate post-fire communities it is not a significant fine fuel component and thus does not have any meaningful effect on fire regimes (Brooks et al., 2018; Underwood et al., 2019).

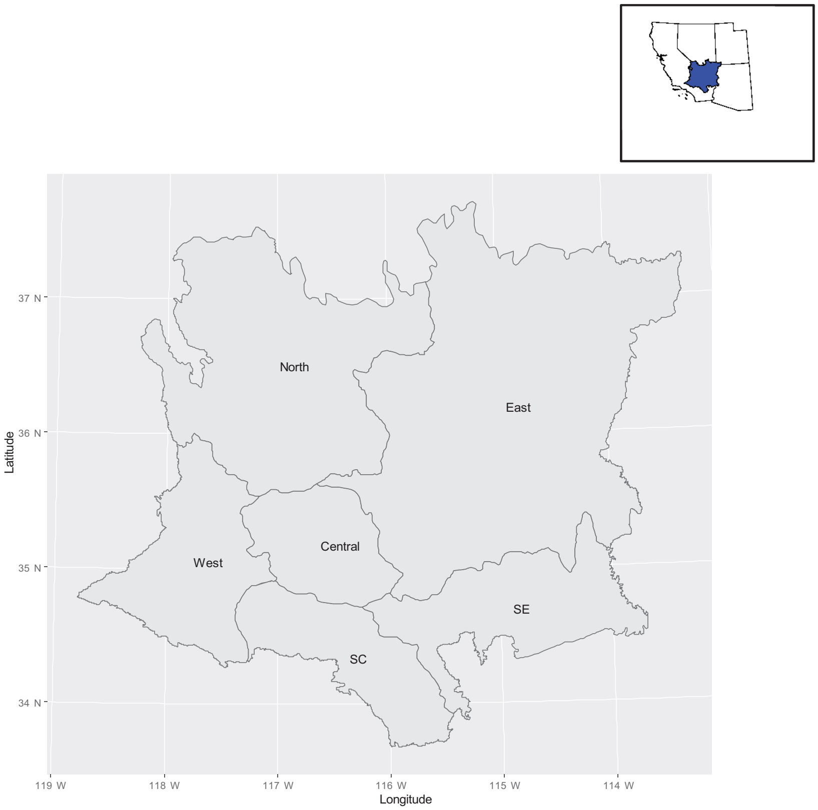

FIGURE 1 | The Mojave Desert of North America. SE, southeastern subregion; SC, southcentral subregion.

Fire Atlas

Data on fire perimeters and burn severity across the Mojave from 1984 to 2010 were acquired from the Monitoring Trends in Burn Severity (MTBS) database[1]. MTBS uses Landsat satellite data to delineate the perimeters and burn severity indices for fires >405 ha (1,000 acres) on all public and private lands across the western United States. Perimeters are identified by comparing pre and post-fire images of the Normalized Burn Ratio (NBR; Key and Benson, 2006; Eidenshink et al., 2007), then burn severity indices (30 m resolution) based on NBR are derived. The indices include the difference Normalized Burn Ratio (dNBR), relativized dNBR (RdNBR), and an ordinal scale (unburned, low, moderate, high, and very high). Non-disturbance related differences between pre and post fire Landsat images can bias comparisons of severity among fires. Therefore, we used an offset to calibrate the dNBR layers to a more equivalent baseline, thereby improving comparisons among multiple individually mapped burn areas (Klinger et al., 2019). The offset (a plus or minus shift to the dNBR values) was based on the mean unchanged pixel value contained within individual MTBS metadata files (identified there as the “RdNBR offset”) and comes from a sample of unchanged pixels outside of the fire perimeter.

Monitoring Trends in Burn Severity data are not available prior to 1984 but Landsat imagery is available back to 1972. Therefore, we extended our time period an additional decade (1972–1983) by accessing Landsat 4/5 Multispectral Scanner (MSS) imagery and then using methods similar to those of the MTBS program to delineate fire perimeters. We selected one high-quality scene for the spring (April, May, and June) and one for the late summer/early fall (August, September, and October) of each year, corresponding to the beginning and end of the Mojave’s fire season. Scenes were selected to minimize cloud cover (<10%) and other anomalies (e.g., missing data and bad lines) that occur sometimes in older Landsat images. Although the images we selected were of high quality, MSS lacks the shortwave infrared (SWIR) spectral band required to derive dNBR and its resolution is coarser (79 m) than that of later Landsat satellites (30 m). Nevertheless, MSS bands do allow the calculation of the difference Normalized Difference Vegetation Index (dNDVI; Petorelli, 2013), which provides comparable estimates of severity as dNBR (Zhu et al., 2006; Hudak et al., 2007). We integrated dNDVI with other geospatial data (digital elevation models, topographic maps, etc.) to identify fire perimeters, and in so doing found the difference in resolution to be a trivial issue for delineating perimeters of the burns.

We calculated fire frequency by using the raster package (Hijmans, 2020) in R (R Core Team, 2019) to overlay the fire perimeters (1972–2010) and sum their overlap. We used

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[1] http://www.mtbs.gov/

dNBR to index burn severity (1984–2010) because it relates very well with changes in ground-based measures of severity (woody cover and density) in the Mojave and has a more direct ecological interpretation than either RdNBR or the ordinal scale (Klinger et al., 2019). Wildfires in the Mojave occur as a result of human and natural ignitions (Hegeman et al., 2014; Brooks et al., 2018), but virtually all large ones (>405 ha) are due to lightning strikes (Brooks et al., 2018). Thus, our atlas of large Mojave wildfires represents those resulting exclusively from natural ignitions.

Environmental Predictor Variables

We identified 15 variables as potential predictors of probability of ignition and frequency of fire, and 13 as predictors of burn severity (**Table 1**). Topography variables were derived from a digital elevation model[2] (30 m resolution) and included elevation, slope, an index of terrain ruggedness (TRI; Wilson et al., 2007), aspect (cosine transformed), and hillshade (an index of localized heating). Five climate variables were derived from the ClimSurf climate surface (Alvarez et al., 2013), including mean wet (October–March 1949–2010) and monsoon season precipitation (July – September 1950–2010), proportion of monsoon season precipitation, mean minimum January temperature (1950–2010), and mean maximum July temperature (1950–2010). Vegetation variables included habitat suitability values for two brome grasses (*B. rubens* and *B. tectorum*), habitat suitability values for two Mediterranean split grass species (*S. arabicus* and *S. barbatus*), and mean growing season NDVI (March – June 1990 – 2010). In a previous study, we found habitat suitability values of the three invasive grass taxa had strong positive correlations with their cover values (Underwood et al., 2019). Therefore, we extracted the suitability values from maps developed in that study as a region wide proxy to their abundance. Although peak cover values of the grasses diverge with elevation, the bromes overlap from ≈1,400—2,000 m and distributions of the split grass species are almost indistinguishable (Underwood et al., 2019). However, overlap between the bromes and split grass species is limited (Underwood et al., 2019). This suggested that it was appropriate to combine bromes together (Bromes) and split grass together (Schismus), but these two variables should be separate predictors (**Table 1**). NDVI values were derived from the USGS Analysis Ready Data (ARD) database (Dwyer et al., 2018). ARD are produced from Landsat 4–8 satellite images that have been accurately georegistered, calibrated, and pre-processed (top of atmosphere and atmospheric correction).

We acquired lightning strike point data beginning in January 1990 and ending in December 2010 from the National Lightning Detection Network (NLDN) accessed through NOAA-NCEI[3]. Data included the geographic coordinates of the strikes, the date, and polarity (amperes with positive or negative charge). We calculated the density of strikes by dividing the region into 10 km × 10 km blocks, summed the number of positive and negative strikes in each 100 km^2 block, and then calculated the mean per block (1990–2010). We calculated positive and negative strike densities separately because negative strikes are 10–20× more frequent than positive strikes, but positive strikes have 1–2 orders magnitude greater energy than negative strikes. This creates the potential for lightning regimes differing in strike intensity and energy.

All processing of the environmental variables was done in R. We used the raster package to derive the topographic variables, the greenbrown package (Forkel et al., 2013, 2015) to derive mean growing season values for NDVI, and the spatstat package to calculate lightning density (Baddeley et al., 2015). The climate and lightning rasters were resampled to a resolution of 30 m.

Spatial Analysis of Fire Frequency 1972–2010

We used point process models (PPMs) to analyze the spatial distribution of fire frequency. PPMs are a regression approach for modeling point data (i.e., geographic coordinates) for an event, which in our case was how frequently a local area (30 m pixel) had burned between 1972 and 2010. PPMs are closely related to generalized linear models (GLMs) but differ in that they model the intensity of points (i.e., points per unit area) rather than the level of a random response variable (Baddeley et al., 2015). Models can be specified that assume a Poisson process where intensity is constant across a study area (homogenous point process) or, much more typically, where intensity varies because environmental conditions are not uniform (inhomogenous point process). Thus, the relationship that intensity (λ) has with geographic position (spatial trend) and/or environmental variables can be modeled as in regression, with predicted values having a direct interpretation as a measure of points per unit area.

When points are assigned attributes they are known as marked. We converted our raster data to points by calculating the centroid of each pixel and assigned each point one of three marks f based on the number of times it had burned from 1972 through 2010: once (=1), twice (=2), or >2 times (=3). We then specified and compared five models of λ_f: (1) an interaction between λ_f, spatial trend, and the second-order effect of elevation; (2) an interaction between λ_f, spatial trend, and the linear effect of elevation; (3) the interaction of λ_f, and spatial trend; (4) the interaction of λ_f, and the second-order effect of elevation; and, (5) the interaction of λ_f, and the linear effect of elevation. The models were based on a non-stationary Gibbs process, where λ_f, was a log-linear function with spatial dependence among points. We included the second-order effect of elevation because previous studies had reported fire activity was greatest in the mid elevation zone of the Mojave (Brooks and Matchett, 2006; Tagestad et al., 2016). PPMs are computationally intensive and large values can prevent them from converging, therefore we rescaled the spatial coordinates (Universal Transverse Mercator) and elevation values by subtracting their mean and dividing by their SDs (standardization).

It was computationally prohibitive to use all of the fire frequency data points ($>7 \times 10^7$) in one analysis, so we used

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[2] https://www.sciencebase.gov/catalog/item/4f70aa71e4b058caae3f8de1

[3] https://www.ncdc.noaa.gov/data-access/severe-weather/lightning-products-and-services

TABLE 1 | Potential predictor variables in models of probability of ignition, fire frequency, and burn severity (difference normalized burn ratio; dNBR) in the Mojave Desert of North America.

			Models where included		
Predictor variable	**Code**	**Group**	**Ignition**	**Frequency**	**dNBR**
Elevation	Elevation	Topography	1	1	1
Slope[1]	Slope	Topography			
Terrain Ruggedness Index	TRI	Topography	1	1	1
Hillshade	Hillshade	Topography	1	1	1
Aspect[2]	Aspectcos	Topography			
Mean minimum January temperature[3]	Tmin01	Climate			
Mean maximum July temperature[3]	Tmax07	Climate			
Mean wet season precipitation	PPTWint	Climate			1
Mean monsoon season precipitation[4]	PPTMons	Climate			1
Mean annual proportion monsoon precipitation	PropMons	Climate	1	1	1
Habitat suitability for Brome grasses[5]	Bromes	Vegetation	1	1	1
Habitat suitability for Mediterranean split grass[5]	Schismus	Vegetation	1	1	1
Normalized difference vegetation index	NDVI	Vegetation	1	1	1
Density of negatively charged lightning strikes[6]	Strikes100Neg	Lightning			
Density of positively charged lightning strikes[7]	Strikes100Pos	Lightning			
Derived from above variables					
Mean annual precipitation[8]	Precip	Climate	1	1	
Density of lightning strikes[9]	Lightning	Lightning	1	1	1

1 = variable was included in final model

[1] *Not included because of strong correlation with TRI (r = 0.983).*

[2] *Not included in final models because of negative variable importance values.*

[3] *Not included because of strong correlation with elevation (r = −0.891).*

[4] *Not included in ignition and frequency models because of strong correlations with Strikes100Neg (r = 0.875) and Strikes100Pos (r = 0.870).*

[5] *Extracted from models of habitat suitability for red brome, cheatgrass, and Mediterranean split grass (Underwood et al., 2019).*

[6] *Not included because of strong correlation with Strikes100Pos (r = 0.915).*

[7] *Not included because of strong correlation with Strikes100Neg (r = 0.915).*

[8] *PPTWint + PPTMons.*

[9] *Number of lightning strikes per 100 km^2; Strikes100Neg + Strikes100Pos.*

non-parametric bootstrapping for parameter estimation. We randomly selected 10,000 points without replacement in each of 200 bootstrap samples and ran each model for each sample. We used Akaike's Information Criterion (AIC) to compare models and selected the one whose AIC weight (*w*AIC) was >0.90 (Burnham and Anderson, 2002). Final parameter estimates and 95% CIs were based on the mean of the 200 bootstrap samples and the 2.5 and 97.5% quantiles of the distribution of parameter values, respectively. We used the R package spatstat (Baddeley et al., 2015) to conduct the PPMs.

We used a modification of resource selection ratios (Manly et al., 2002) to evaluate the occurrence of fire relative to the area of three elevation zones: low ($\leq$1,200 m), mid (1,201–1,700 m), and high ($>$1,700 m). The analysis used the proportion of area in each elevation zone *z* throughout the Mojave ("available") and the proportion of area in each elevation zone that burned to construct a ratio $W_z = \text{burned}_z/\text{available}_z$. We used an omnibus log-ratio test to first determine if fire occurred disproportionally across the zones, followed by *z*-tests for each zone to evaluate those that had disproportionally more or less fire activity. A second index *B* was constructed as $B_z = W_z/\Sigma W_z$, which allowed us to compare fire occurrence in a given zone relative to a "baseline" zone. The zones corresponded to the major vegetation types in the Mojave (Brooks et al., 2018; Klinger et al., 2019): low elevation shrubland typically dominated by creosote bush (*Larrea tridentata*) and burroweed (*Ambrosia dumosa*); mid-elevation shrubland dominated by blackbrush (*Coleogyne ramosissima*), snakeweed (*Gutierrezia sarothrae*), Mormon tea (*Ephedra nevadensis* and *Ephedra viridis*), and turpentine broom (*Thamnosma montana*); high elevation woodland and shrubland dominated by sagebrush (*Artemisia tridentata*), antelope bush (*Purshia tridentata*), juniper tree (*Juniperus osteosperma*), and single-leaf pinyon (*Pinus monophylla*). We reasoned that if fire occurred more than expected in an elevation zone this was consistent with there being higher fuels, greater rates of ignition, or both. If fire was less than expected this was consistent with a zone having sparser fuels, lower ignition rates, or both. If fire occurred proportional to the area of a zone this would be consistent with burning being area dependent more so than strong effects from either fuels or ignition. We used a similar approach as we did with the PPMs, with 10,000 random samples drawn without replacement for each of 500 bootstrap samples.

Modeling Probability of Ignition

While it would be reasonable to expect that probability of ignition (i.e., the likelihood of a fire starting) and fire frequency would have a positive correlation, this may not always be so in the

Mojave because of the high heterogeneity in topography and, especially, fuel type (Brooks et al., 2018). Therefore, we developed separate models for probability of ignition and fire frequency.

Maximum Entropy (Maxent) modeling was used to calculate the probability of ignition across the Mojave. Maxent is a machine learning algorithm that contrasts the conditions at locations where an event is known to have occurred with those at background locations (Phillips et al., 2006). It is one of the most widely used predictive modeling algorithms for studies in the environmental sciences, especially those focused on species distributions (Elith et al., 2011). Over the last decade it has seen increasing use in studies examining how vegetation, climate, and human activities influence fire activity (Parisien and Moritz, 2009; Batllori et al., 2013; Syphard et al., 2013; Parisien et al., 2016; Martin et al., 2019). Maxent iteratively adjusts the probabilities of a uniform (null) distribution based on the predictor variables at each location. The iterations stop when the distribution becomes one with maximum entropy, which is the best approximation of how the predictor variables change the null distribution (Elith et al., 2006). The final output is an exponential function that assigns a predicted value proportional to the probability of occurrence to each site or cell of a map (Renner and Warton, 2013). Maxent has several beneficial features, including the ability to model complex functional relationships between response and predictor variables, quantification of the relative importance of the predictor variables, and the capability to adjust calculations to avoid overfitting (regularization; Phillips and Dudik, 2008).

To implement the Maxent model we used the dismo package in R (Hijmans et al., 2017) as an interface to the MAXENT package (Phillips and Dudik, 2008). Fire occurrence was the response variable and there were 15 potential predictor variables (**Table 1**). We randomly selected a total of 10,000 points separated by ≥90 m and sampled proportional to the area of the fire perimeters, then extracted the values of the predictor variables at each point. We did a preliminary analysis of the pairwise correlation among the predictor variables and removed one of each pair with a correlation (r) $\geq$ 0.70, resulting in N = 10 standardized predictor variables (**Table 1**).

We used 10-fold cross-validation to partition the response variable into training and test data sets and then calculated the mean and SD of the Area Under the Curve of the Receiver Operator Characteristic (AUC from hereon) as a threshold independent measure of model performance. Because there is potential for AUC to be biased (Lobo et al., 2007), we evaluated the values in our partitions using point-wise distance sampling (Hijmans, 2012). We used 10,000 randomly selected background points in each model partition. The response and background points were divided into training (70%) and test sets for each fold.

Two approaches were used to evaluate importance of the predictor variables. The first was calculated as the increase in prediction gain when the coefficient for each variable was changed. The amount of change is summed for each variable and expressed as a percentage of the total gain (Phillips and Dudik, 2008). The second approach consisted of jackknifing to calculate: (1) the decrease in training and test gain when a variable was removed from a model; and, (2) the highest training and test gain when a variable was the only one in a model (Phillips and Dudik, 2008).

Modeling Fire Frequency and Burn Severity

We used Random Forests (RF from hereon; Breiman, 2001) to evaluate how effectively the environmental variables predicted fire frequency and burn severity. RF is a supervised machine learning algorithm that extends the capabilities of classification and regression trees (CART; Olden et al., 2008). It recursively creates many trees from bootstrap samples of the dataset and compares the predictions of each tree to the data not in that bootstrap sample (the validation or "out-of-bag" sample). In effect, this creates numerous internally cross-validated models. Unlike CART the trees are not "pruned"; instead, each develops to its full extent. Variable importance is calculated by randomly permuting the values of each variable one at a time within each recursive run and calculating change in model performance. Final predictions and accuracy estimates are calculated by averaging the predictions of all the trees. Prediction values are the probability of belonging to a particular class (fire frequency = 1, 2, etc.) or, for continuous response variables (dNBR), an estimate of the response variables value.

Random Forests has many strengths. Each of the realizations of the recursions not only uses a different random subset of the data but also a different random subset of the predictor variables, which inherently makes it an ensemble modeling procedure. The algorithm processes high-dimensional data efficiently and it avoids overfitting data, outliers and spatial autocorrelation have much less influence on predictions than in parametric models, and complex non-linear relationships can be revealed. There are tradeoffs though relative to parametric models. It is non-parametric so there are no regression coefficients with measures of uncertainty, which is one of the principal issues in criticisms of using RF (or machine learning in general) for explanatory models (Humphries et al., 2018). Individual trees cannot be examined, which gives a perception of the algorithm being a black box. Despite these concerns, RF has become increasingly recognized as one of the most useful and effective machine learning algorithms when prediction is the primary goal of a study (Cutler et al., 2007; Crisci et al., 2012).

Our data consisted of a random selection of 20,000 points each within and outside the fire perimeters, with a minimum distance between sample points ≥90 m. Samples from within the perimeters were stratified by the area of the polygons. We split the points into training (75%) and test (25%) data sets. The training data were then partitioned with 10-fold cross-validation, with model runs for each partition k split into training (70%) and out-of-bag (OOB from hereon) sets. Fire frequency was divided into four classes based on the number of times a pixel had burned between 1972 and 2010: Unburned (=0), 1 burn (=1), 2 burns (=2), and more than 2 burns (>2). We used the same set of potential predictor variables in the fire frequency models as we did with the probability of ignition models (**Table 1**). We did not include lightning in the models for dNBR because it would have little if any effect on burn severity, and only data from within the fire perimeters were used in the dNBR model runs.

Model development consisted of three steps. We first tuned a model to determine the total number of trees and the optimal number of predictor variables to include at each split in the trees. We then ran an initial model using all of the predictor variables and evaluated it based on three criteria: (1) stability of the model mean squared error (MSE) as the number of trees increased; (2) the minimum MSE of the cross-validations for models with N variables; and, (3) the sign (positive or negative) of the variable importance values. Variable importance was evaluated by the proportional increase in MSE when a variable was not included in the models. If the sign of the importance value was negative this indicated the variable should be removed. The third step for the fire frequency models consisted of running a model with the optimal number of variables. The third step for dNBR models was comparing the pseudo-R^2 ($1 - [\text{MSE}/\sigma^2\text{dNBR}]$) values for those without topography variables, without climate variables, and without vegetation variables to the pseudo-R^2 for models with topography, climate, and vegetation variables.

We used three sets of information to evaluate the performance of the fire frequency model: (1) the OOB error rate; (2) classification success from a confusion matrix of the observed and predicted frequency classes in the training and test datasets; and, (3) AUC values for pairwise classification of frequency classes (e.g., Unburned vs. 1 burn, Unburned vs. 2 burns) in training and test datasets. dNBR models were evaluated with: (1) pseudo-R^2; (2) the absolute differences in observed and predicted dNBR values in the training and test datasets; and, (3) proportional differences calculated from the log-ratios of observed and predicted dNBR values in the training and test datasets. The randomForest package in R was used to develop and evaluate the models (Liaw and Wiener, 2002).

Association of Burn Severity With Probability of Ignition and Fire Frequency

We used two approaches to examine the association between probability of ignition and dNBR. First, a PPM was developed that enabled us to contrast the spatial trends in the predicted values of the two variables. We classified the continuous predicted variables into five evenly spaced quantiles, then specified an interaction model with the classes as marks and the spatial coordinates as predictor variables. We estimated the coefficients and their SEs from 250 non-parametric bootstrapped samples ($N = 500$ per sample), then compared the sign and magnitude of the coefficients between the probability of ignition and dNBR model runs. The models were based on a non-stationary Gibbs process and the spatial coordinates were standardized.

Next, we used a combination of redundancy analysis (RDA; Legendre and Legendre, 1998) and permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to evaluate variation in probability of ignition and dNBR among the six Mojave subregions (Webb et al., 2009). RDA is a constrained form of Principal Components Analysis (PCA) that relates the variation among multiple response variables to a set of predictor variables. PERMANOVA is a non-parametric multivariate technique that compares both the centroids and dispersion among different groups. Conceptually, RDA and PERMANOVA are related in a similar way as linear discriminant analysis (LDA) and multivariate analysis of variance (MANOVA). However, LDA and MANOVA are least squares methods where group differences are tested against probability distributions. In contrast, RDA and PERMANOVA are based on distance matrices and group differences are evaluated by Monte Carlo permutation tests, freeing them from the restrictive assumptions of least squares-based methods.

For the PERMANOVA we specified probability of ignition and dNBR as response variables and subregion (North, East, Southeast, Southcentral, West, and Central) as the predictor variable. We randomly selected 500 points in each subregion and then extracted the probability of ignition and dNBR values for each point. We derived a Euclidean distance matrix and tested if there were differences among the subregions with Monte Carlo permutation tests ($N = 999$). PERMANOVA is sensitive to differences among groups in location (group centroids) and dispersion (variance; Anderson, 2001), therefore we conducted a permutation-based test of multivariate homogeneity of group dispersions and a *post hoc* Tukey test to help interpret patterns of difference among the subregions. We then performed the RDA to visualize positions of the subregions in multivariate space. We tested the significance of the RDA with Monte Carlo permutation tests ($N = 999$) and derived centroids for the subregions as well as ellipses of the centroid SEs and 95% confidence bounds to evaluate the interplay between location and dispersion among subregions. The vegan package in R (Oksanen et al., 2020) was used to conduct the PERMANOVA and RDA.

We used ordinary least-squares (OLS) regression to model the relationship between predicted values of dNBR and fire frequency along an elevation gradient. We selected 1,000 random points in each frequency class (1, 2, and >2 burns from 1972 through 2010) and used the raster package in R to extract values of dNBR, frequency, and elevation at each point. We specified dNBR as the response variable and an interaction between the frequency classes and the 2nd-order effect of elevation as the predictor variables.

RESULTS

Spatial Pattern of Burning

We identified 250 fires (>405 ha) totaling 753,288 ha that occurred between 1972 and 2010 (**Figure 2**). This comprised 5.8% of the total area of the Mojave, with the vast majority burning only once; <1% of the total area of the Mojave had burned two or more times (**Table 2**). The distribution of area burned among the fires was highly skewed, with 83% occurring from fires between 412 and 5,000 ha (**Figure 3**). However, three fires > 50,000 ha each occurred in 2005, comprising 29% of the total area burned between 1972 and 2010.

The PPM that included the interaction between λ_f, spatial trend, and the second-order effect of elevation had complete support; it was the highest ranked model in each bootstrap

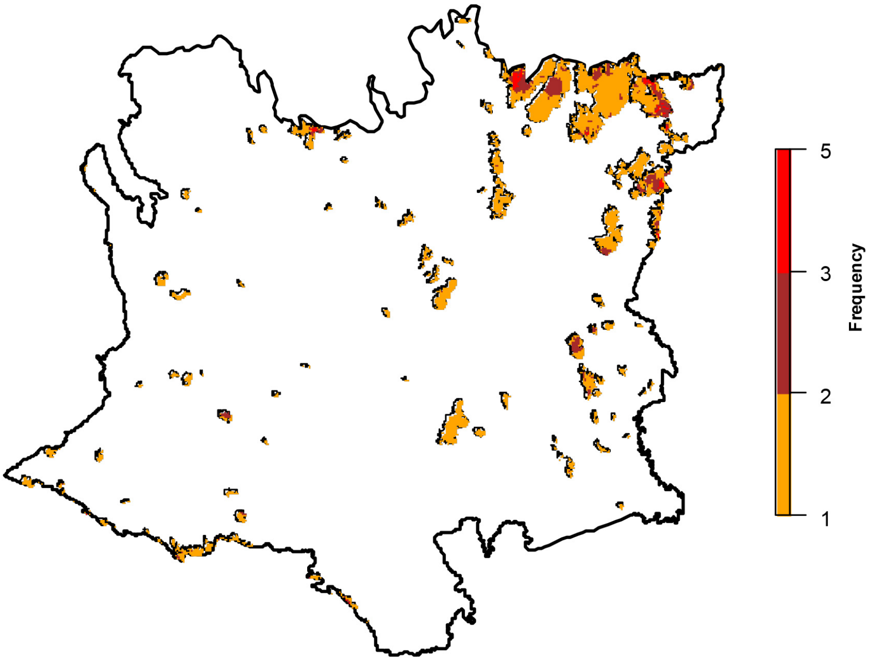

FIGURE 2 | Fire perimeters classified by fire frequency (number of times burned from 1972 to 2010; 1, 2, and >2) for 250 fires >405 ha in the Mojave Desert of North America.

sample (N = 200), wAIC = 1 in each sample, and none of the parameters overlapped zero (**Supplementary Table 1**). The model indicated clear structuring in the spatial distribution of the fires (**Figure 4**). There was a distinct increasing southwest to northeast trend for all three frequency classes, especially when fire frequency $\geq$ 2. An overwhelming majority of pixels that burned twice and virtually all that burned three or more times clustered in the Eastern subregion. Intensity of pixels that had burned once also clustered strongly in the Eastern subregion, but clusters of similar intensity occurred in mountain ranges in the Western, Southern, and Central subregions as well. Intensity of burned pixels peaked at mid-elevations for all three frequency classes (**Figure 5**). Fire occurred 1.4 and 2.7× more than expected in the high and mid elevation zones, respectively, but was 1.8× less than expected in the low elevation zone (**Supplementary Table 2**). Relative to the low elevation zone, fire was 3–5× greater in the high and mid elevation zones, respectively (**Supplementary Table 2**).

TABLE 2 | The number and proportion of hectares burned in fires >405 ha in the Mojave Desert of North America, 1972 – 2010.

		Proportion burned	
Frequency	**Hectares**	**Burn area**	**Mojave**
1	636528	0.845	0.049
2	98681	0.131	0.008
3	15819	0.021	0.001
4	1507	0.002	<0.001
5	753	0.001	<0.001
Total	753288		0.058

Frequency is the number of times a pixel (30 m) burned during that period of time. Burn Area is the proportion within the fire perimeters (N = 250) and Mojave is the proportion of the region (13,059,918 ha).

Probability of Ignition

The AUC values were 0.967 (SD = 0.001) for the Maxent training data model and 0.964 (SD = 0.002) for the test data model (**Supplementary Figure 1**). Bromes, lightning, NDVI, and Schismus comprised 96% of the contribution to predictions in the training data model and 94% in the test data model (**Supplementary Table 3**). Bromes alone accounted for 63% of the contribution to predictions in both the training and test data (**Supplementary Table 3**). There was little measurable influence on either training or test gain when variables were individually removed from the models, but meaningful increases in both training and test gain occurred when Bromes, lightning, NDVI, or precipitation were the only variables in a model (**Supplementary Table 3**).

The pattern of predicted probability of ignition was one of high heterogeneity (**Figure 6**). A large portion (68%) of the Mojave had ignition probabilities > 0.20, but these areas varied in size and continuity throughout the region. Consistent with the variable importance rankings, values of probability of ignition were highest in the more mountainous parts of the region, especially in the East subregion (**Figure 6**). Other than the fringing mountain ranges, extensive parts of the West, Central and North subregions had low to moderate predicted values (**Figure 6**).

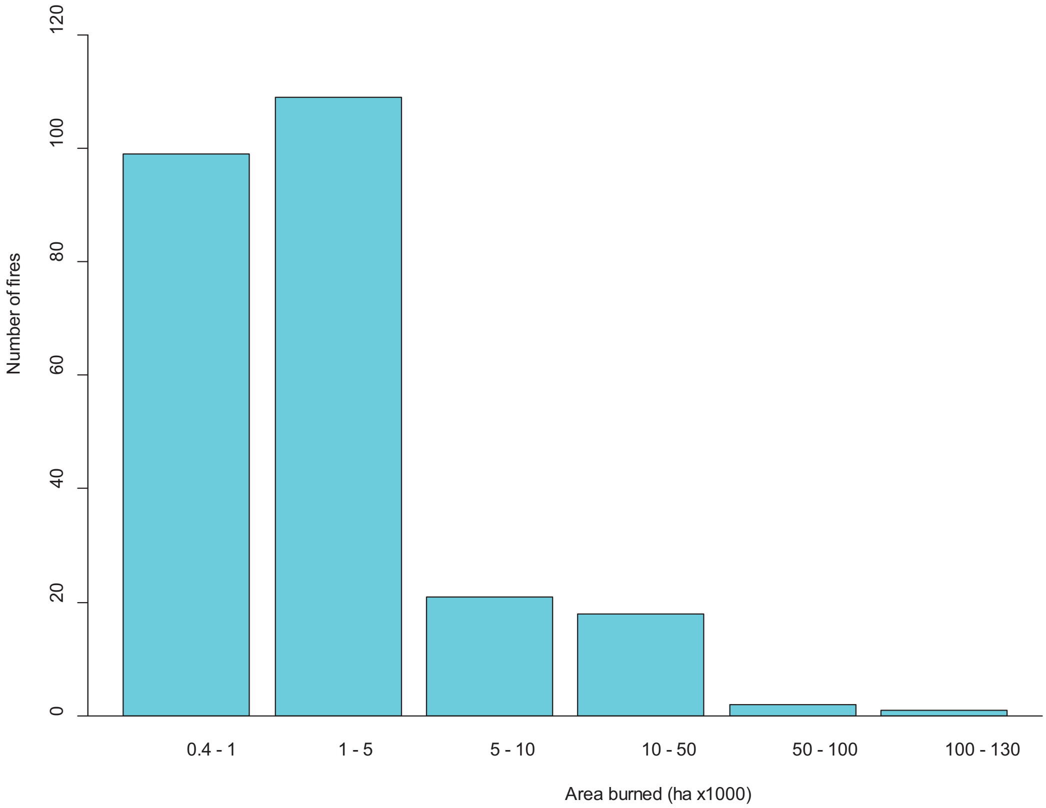

FIGURE 3 | Distribution of the area within the perimeters of 250 wildfires that burned in the Mojave Desert of North America from 1972 through 2010.

Fire Frequency

Tuning of the RF model of fire frequency resulted in 250 trees with 6 predictor variables at each split in the trees (**Supplementary Figure 2A**). Overall classification accuracy of the fire frequency classes was 0.851 for the training data and 0.842 for the test data. Classification accuracy in the training and test datasets > 0.92 for unburned and 1 burn classes and was approximately 0.80 for the >2 burn class (**Table 3**). Classification accuracy for 2 burns was the lowest of the four classes in both training and test datasets, with most misclassifications occurring in the 1 burn class (**Table 3**).

Seven of the predictor variables had markedly more importance than the remaining three (**Figure 7**): proportion of monsoon precipitation, Bromes, lightning strikes, NDVI, elevation, total annual precipitation, and Schismus. None of the predictor variables had negative values, but the three with the lowest importance were all topographic variables (**Figure 7**). The 10-fold cross validation indicated that there was little difference in mean-squared error for models with ≥ 4 predictor variables (**Supplementary Figure 3**), therefore we selected a final model consisting of the test data and the seven predictor variables with the highest importance values. Pairwise AUC values for the predicted fire frequency classes were all ≥ 0.885 (**Supplementary Table 4**), with overall AUC = 0.963.

Fire frequency was predicted to be highly heterogenous throughout the Mojave (**Figure 8**). Notably, many areas where frequency was predicted to be high had not actually burned since at least 1972. This resulted in the area predicted to be susceptible to burning being considerably greater than what actually occurred between 1972 and 2010 (compare **Figures 2**, **8**). Although areas predicted to have high fire frequency occurred patchily throughout the region, large areas where fire frequency >1 were clustered primarily in the East subregion (**Figure 8**).

Burn Severity

Tuning of the RF model of dNBR resulted in 250 trees with 3 predictor variables at each split in the trees (**Supplementary Figure 2B**). Pseudo-R^2 values were higher for models that included variables from the topography, climate, and vegetation groups as opposed to models where variables from one of the groups were omitted (**Supplementary Table 5**). The importance value for aspect in the initial model runs was negative, therefore it was removed from subsequent model runs. The remaining variables all increased prediction success, with NDVI and the proportion of monsoon precipitation having the highest importance values (**Figure 7**).

The mean differences between observed and predicted dNBR values were −3 in the training dataset and −4 in the test dataset (median = −7 in both training and test datasets). Proportionally, the mean differences were within 6% of the actual values (median = −3% in both training and test datasets). Half of the predicted values occurred between −39 and 30 in the

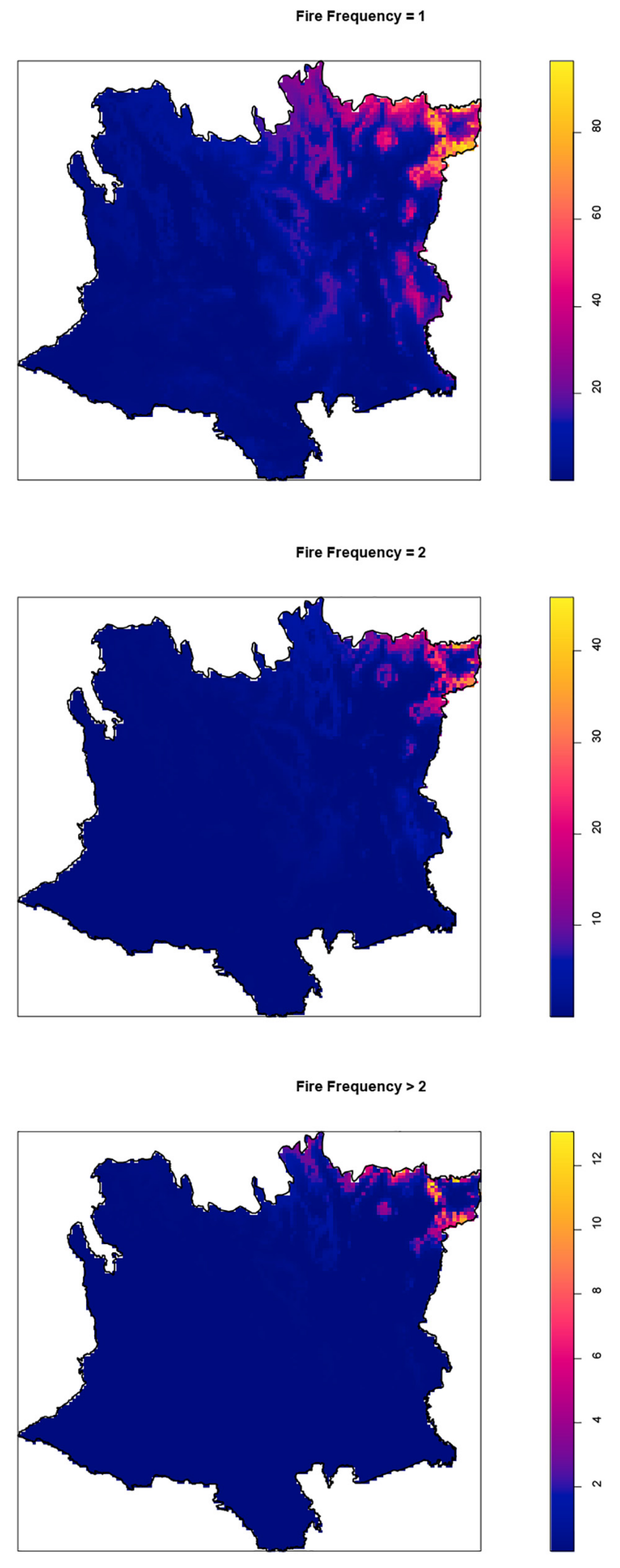

FIGURE 4 | Predicted density of fire occurrence (number of burned pixels 100 km^2) in three fire frequency classes (number of times burned from 1972 to 2010) in the Mojave Desert of North America. Density was estimated with a point process model of 250 wildfires.

training dataset and 38 and 30 in the test dataset (**Supplementary Figure 4**); proportionally this was equal to being within −24 to 14% of actual values in both training and test datasets (**Supplementary Figure 5**). 95% of the predicted values were between −91 and 107 in the training dataset and −90 and 99 in the test dataset; proportionally this was equal to being within −68 to 33% of actual values in both the training and test datasets.

Approximately 75% of the Mojave was predicted to have low to moderate levels of burn severity (**Table 4** and **Figure 9**). Higher levels of dNBR were predicted to occur principally in mountainous parts of the region, especially in the North subregion (**Figure 9**).

Associations Among Burn Severity, Probability of Ignition and Fire Frequency

There was a moderately high level of correlation between probability of ignition and fire frequency ($r = 0.785$). Mean probability of ignition in the 1-burn frequency class was 0.082 ($SE = 0.005$), while those in the 2-burn and >2-burn classes were 0.450 and 0.648, respectively ($SE = 0.005$ and 0.007).

Almost two-thirds of the Mojave was predicted to have low fire frequency and burn severity (**Table 4**). Areas with moderate to high predicted burn severity comprised 11.5% of the area of the Mojave when probability of ignition was low (quantile = 0–0.25; **Table 4**). This was 2.5× greater than the proportion of area when probability of ignition was in a moderate range (quantile = 0.26–0.50; **Table 4**). Areas where probability of ignition and burn severity were predicted to be high comprised <1% of the region, and areas where probability of ignition and burn severity were predicted to be very high were virtually non-existent (**Table 4**).

The PPMs indicated that probability of ignition and dNBR had distinctly different spatial trends (**Supplementary Table 6**). The sign of the coefficients for longitude differed between ignition probability and dNBR, as did those for the interaction of longitude and the two highest quantiles of ignition and dNBR (**Supplementary Table 6**). Density of ignitions had an increasing southwest to northeast spatial trend, especially for the highest quantile of predicted values (**Figure 6** and **Supplementary Table 6**). In contrast, there was a strong increasing southeast-to-northwest trend in dNBR (**Figure 9**). Overlap in areas where there were higher predicted values of ignition and dNBR occurred principally in the North subregion and several of the interior mountain ranges (**Figures 6, 9**).

The subregions differed in their positions in ordination space (PERMANOVA $F = 122.31$, $df = 5$, $P = 0.001$). The Tukey HSD test pointed toward most differences resulting from separation of the Northern and Eastern subregions from the others (**Supplementary Table 7**). The Southcentral and Central subregions also differed from one another, but there was no meaningful divergence among them and the West subregion (**Supplementary Table 6**). The dispersion test indicated that heterogeneity in variance contributed to differences among the subregions ($F = 130.88$, $df = 5$, $P = 0.001$). This was also apparent in the RDA, where the 95% confidence ellipses of the Northern and Eastern subregions were markedly larger than those in other subregions (**Figure 10**). The first RDA axis accounted

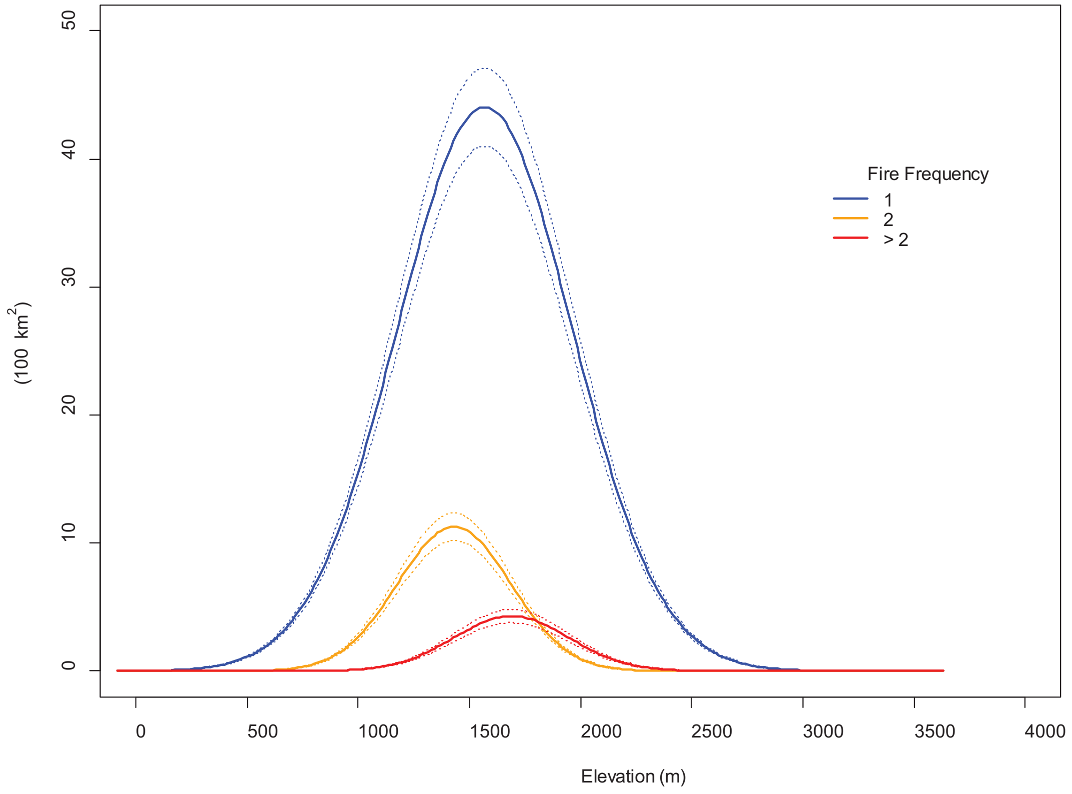

FIGURE 5 | Density (λ; ± 95% CIs) of pixels in three classes of fire frequency (number of times burned from 1972 to 2010) along an elevation gradient in the Mojave Desert of North America.

for 71% of the variation among the subregions (*P* = 0.001) and represented a gradient in dNBR, while the second axis represented a gradient in ignition. The 95% confidence ellipses overlapped among the subregions but the ellipses for their SEs were completely separate. In tandem with the dispersion test, this indicated that the subregions differed in both location and variance. The first axis separated the East, West, and North subregions from the others, with the East having lower dNBR and higher ignition probability values than the West and North subregions (**Figure 10**). The other subregions had lower values for both probability of ignition and dNBR.

The OLS model accounted for 79% of the variation in dNBR due to the interactive influences of fire frequency and elevation (**Supplementary Table 8**). Predicted values of dNBR were consistently higher in the 1-burn class than the 2-burn and >2-burn classes, though the differences were larger at lower and mid elevations than at higher elevations (**Figure 11**). dNBR values in the 1-burn and 2-burn classes increased monotonically with elevation, while those in the >2-burn class peaked at mid-elevations (**Figure 11**).

DISCUSSION

The observed and predicted patterns for fire frequency, burn severity and probability of ignition indicated the occurrence of multiple spatially structured fire regimes throughout the Mojave Desert. The regimes were characterized by an interaction between fire frequency and the degree of burn severity, with the interaction strengths of the two factors being largely opposite each other. Variables that were related to climate and vegetation were important predictors of both frequency and severity, while variables related to topography had importance principally in predicting burn severity. The extent of the GFC is currently limited, but there appears to be great potential for it to become far more widespread.

Two of the most ecologically significant regimes included one characterized by frequent fire (two or more burns every 40–50 years) primarily of low to moderate severity, and another by infrequent fire (one burn every 50–100 years or more) but of high severity. The high frequency regime appears most likely to occur in the northeast part of the region, and, to a lesser degree, in some of the interior mountain ranges. In contrast, the high severity regime appears most likely to occur in the north and northwest, though it is predicted to occur in some interior mountain ranges as well. Two other regimes of ecological importance are one with relatively high fire frequency and burn severity and another with low fire frequency and burn severity. The high frequency and severity regime is very limited in extent, occurring patchily in some interior mountain ranges as well as some of the ranges fringing the Mojave. In contrast, the low frequency and burn severity regime is the

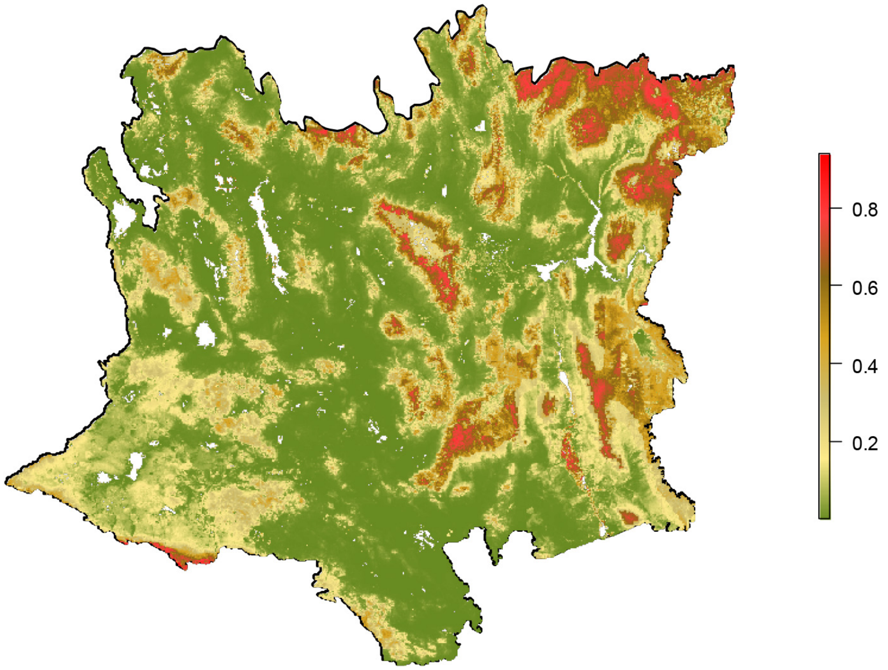

FIGURE 6 | Predicted probability of ignition in the Mojave Desert of North America. Predicted values were derived from a Maxent model (AUC = 0.967 for a test dataset) with 10 variables representing variability in topography, climate, vegetation, and lightning. Because the model was based on background and not true absence data, the predicted values are proportional to true probabilities.

TABLE 3 | Confusion matrix of the proportional classification accuracy for four fire frequency classes (number of fires from 1972 to 2010) in the Mojave Desert of North America.

	Unburned	1	2	>2	Error
Training data					
Unburned	0.939	0.061	0.001	0	0.0615
1	0.045	0.926	0.026	0.004	0.0740
2	0.007	0.233	0.727	0.034	0.2731
>2	0.002	0.089	0.096	0.813	0.1872
Test data					
Unburned	0.947	0.052	0	0	0.0528
1	0.039	0.938	0.020	0.004	0.0619
2	0.014	0.265	0.687	0.034	0.3127
>2	0	0.089	0.115	0.796	0.2038

Error is overall classification error for a given frequency class.

most extensive one in the region, especially in the southern and western parts.

The importance values of the predictor variables provided insight into the spatial structure of fire in the Mojave. Intuitively, probability of ignition and fire frequency would be expected to have positive relationships with sources of ignition and fuels. This was generally the case in the models; Bromes, lightning, NDVI, Schismus, and monsoon precipitation were the highest ranked variables for the probability of ignition model while monsoon precipitation, Bromes, lightning, and NDVI were the highest ranked variables for the fire frequency model. Both monsoon storm activity and biomass of woody vegetation are high in mountainous parts of the region, especially in the east and northeast. Moreover, cover of Brome grasses is high in these areas (Klinger and Brooks, 2017), as is the predicted suitability of their habitat (Underwood et al., 2019). We suspect that the importance of monsoon precipitation has less to do with precipitation than the lightning and high winds that typically occur with the storms (Tagestad et al., 2016). In combination with high woody fuel loads and flammable invasive grasses, lightning and wind dramatically increase ignition, spread and frequency of fires in the eastern and northeastern parts of the Mojave. The south and southeastern parts of the Mojave experience considerable monsoon storm activity but elevations tend to be lower. Thus, the sparser fuels reduce ignitions and limit spread of fire. Fuel loads in the western Mojave can be as high as those in the east and northeast, especially in the mountain ranges bordering the region. Lightning activity is less than in the eastern parts of the region though, limiting ignition probabilities and frequency of fire.

NDVI and the proportion of monsoon precipitation were also important predictor variables in the burn severity model. Their importance makes intuitive sense because burn severity would be expected to be greater in areas with large amounts of biomass available to be removed and where high winds could lead to high fire intensity. However, in contrast with models of probability of ignition and frequency, topography variables had considerable importance in the severity model. The influence of TRI, elevation, and hillshade likely reflects several interactive effects, including local ones of terrain (TRI and hillshade) on fire intensity and

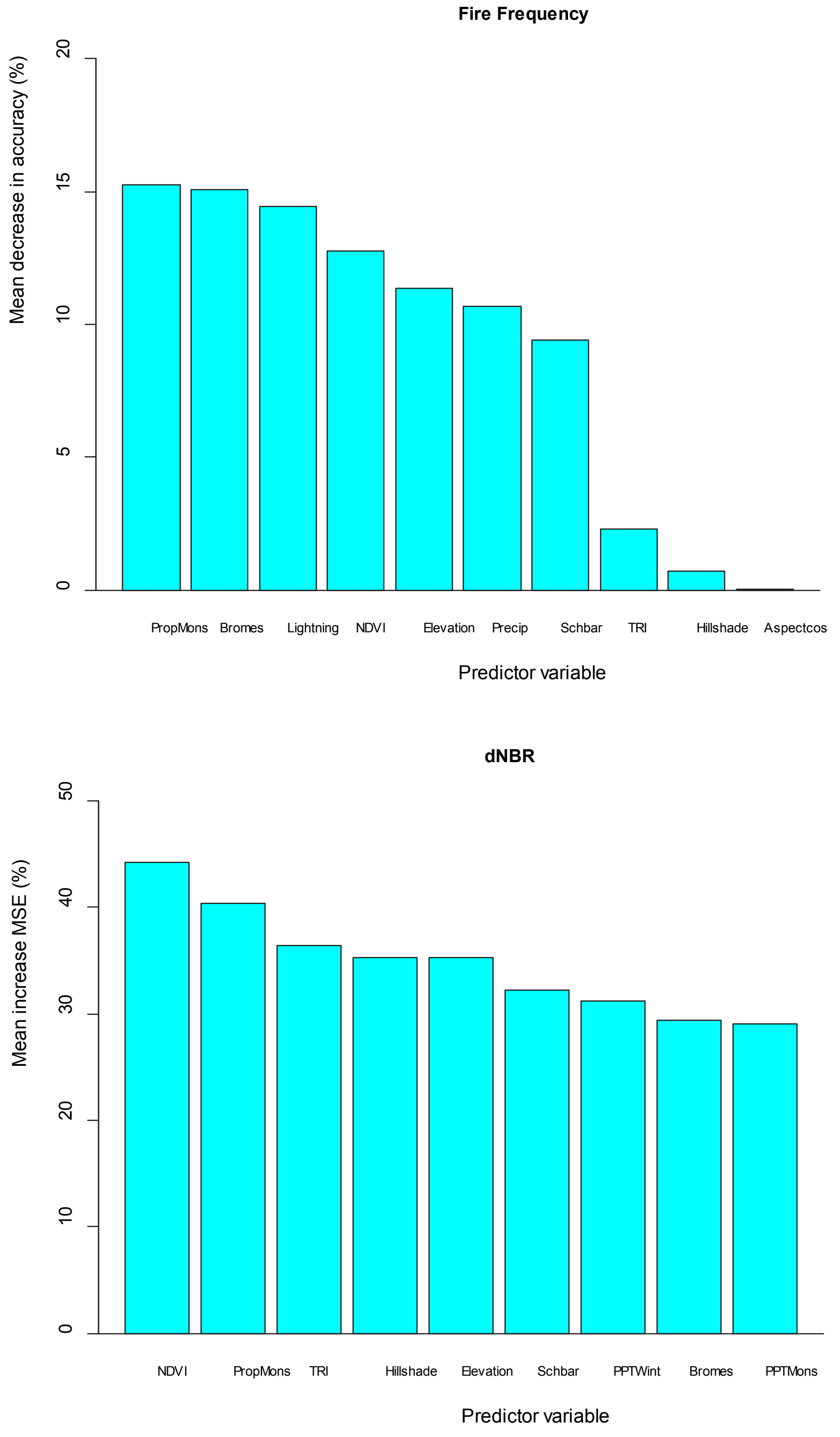

FIGURE 7 | Relative importance values of predictor variables in Random Forest models of fire frequency (number of times burned 1972–2010) and burn severity (dNBR) in the Mojave Desert of North America. Full names and definitions of predictor variables are given in **Table 1**.

spread as well as a larger scale one of elevation on fuel loads and fire spread. There is a strong positive correlation between TRI and slope, and fuel loads and steeper terrain tend to be greater in high than low elevation areas. Steep slopes promote intensity and spread of fire because vegetation is more exposed to both radiant and convective heat. This effect likely compounds

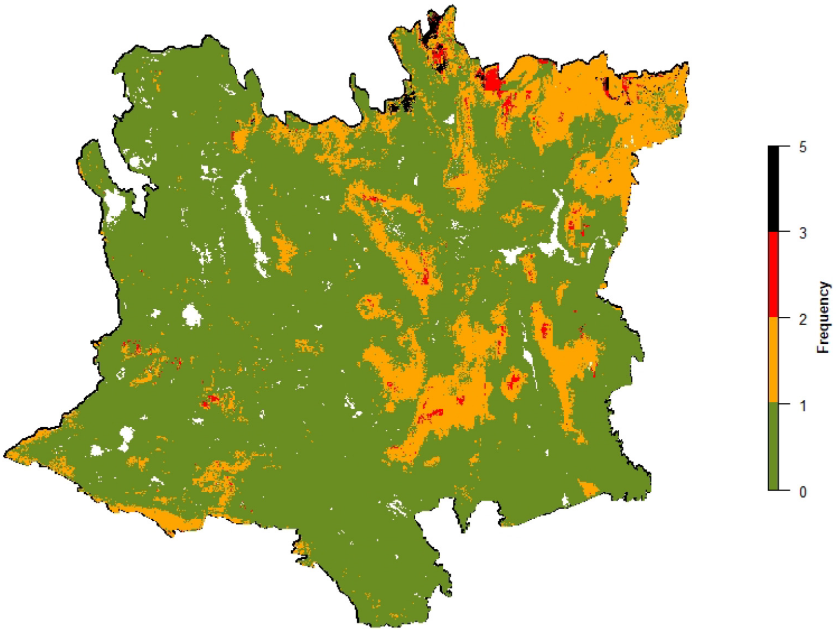

FIGURE 8 | Predicted distribution of fire frequency (Unburned, 1, 2, and >2) resulting from large wildfires in the Mojave Desert of North America. Predictions were derived from a Random Forest model with 10 variables representing variability in topography, climate, vegetation, and lightning.

TABLE 4 | Proportion of area in the Mojave Desert in combinations of predicted quantiles of burn severity (difference normalized burn ratio; dNBR) and ignition probability.

	dNBR quantiles			
	0 – 0.25	0.26 – 0.50	0.51 – 0.75	0.76 – 1
Ignition quantiles	(122 – 228)	(229 – 334)	(335 – 439)	(>439)
0 – 0.25	0.6479	0.1068	0.0078	0.0001
0.26 – 0.50	0.0792	0.0394	0.0045	0
0.51 – 0.75	0.0558	0.0383	0.0026	0
0.76 – 1	0.0038	0.0133	0.0005	0

Ranges of dNBR are listed in parentheses below each quantile.

at larger scales as biomass becomes greater in high elevation areas with steep terrain. A potential exception is in low elevation areas with high biomass of *Schismus* spp. Predictions of dNBR were substantively improved with Schismus as a predictor variable, which we attribute to interspaces among shrubs being filled in by *Schismus* spp. (Brooks, 1999). This increase in *Schismus* biomass would result in higher dNBR values. We stress though that this interpretation is provisional because dNBR tends to be in low to moderate ranges at lower elevations of the Mojave (Klinger et al., 2019).

Brooks and Matchett (2006) hypothesized that fire activity in the Mojave is an outcome of opposing gradients, with lower elevations being largely fuel limited and higher elevations largely ignition limited. Our findings and those of two other studies (Hegeman et al., 2014; Tagestad et al., 2016) are generally consistent with their hypothesis. Nevertheless, it may need to be modified to account for spatial location. The potential for widespread, albeit patchy, high severity fire is considerable due to the mountain ranges that occur throughout the interior of the region. The southeast-to-northwest spatial trend in dNBR values and distribution of wildfires over the last 40–50 years are compelling indications though that this potential has, for the most part, not been realized. This implies spatial structuring in burn severity results mainly from ignitions rather than the distribution of conditions conducive to high severity burns, such as high vegetation biomass. Thus, depending on location, the relative importance of ignition vs. fuel could shift due to local conditions (e.g., low elevation communities with relatively high biomass of invasive grasses or high elevation communities in areas of abundant lightning).

A tradeoff with predictor variables in machine learning models is that they account for non-linear effects and complex interactions better than parametric models do but, because they are non-parametric, their interpretation is less direct. Given this caveat, the importance rankings of the predictor variables in our models generally made ecological sense. Nevertheless, the complex interactions make it inappropriate to infer that statistical rankings translated directly to ecological rankings. For instance, precipitation is known to be one of the most important influences on fire in the North American deserts (Brooks and Matchett, 2006; Balch et al., 2013; Hegeman et al., 2014; Tagestad et al., 2016; Chambers et al., 2019; Underwood et al., 2019), but in our models it had intermediate or even low rankings. It would be wrong though to think this was an indication that precipitation was of lesser importance for fire activity in the Mojave. First, its effects on fire are expressed indirectly through mediation of vegetation biomass. This was well represented in our models by NDVI and, to a lesser degree, by the Bromus and Schismus

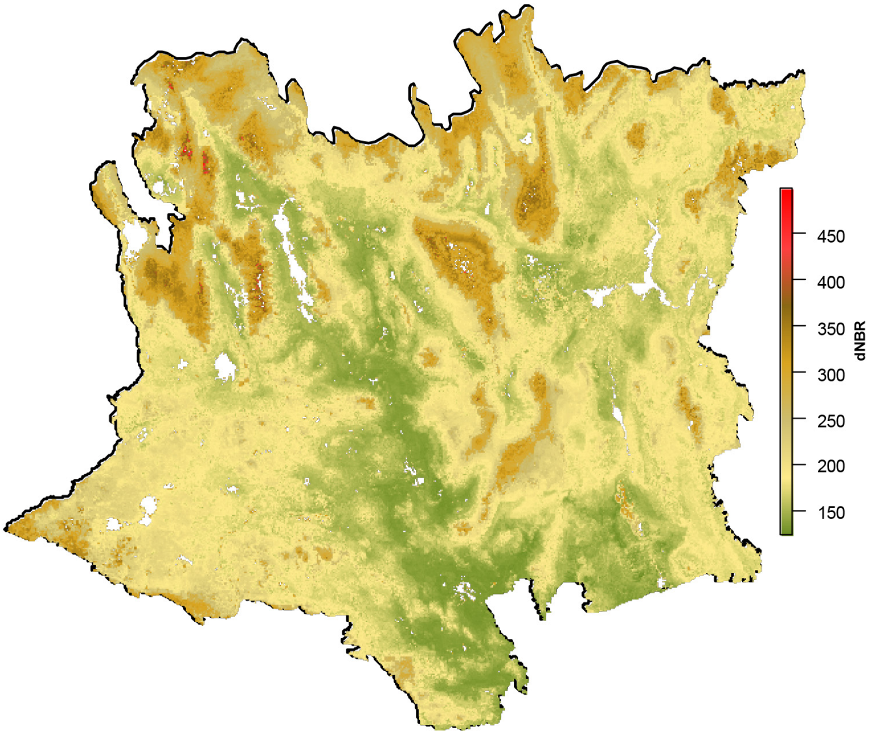

FIGURE 9 | Predicted values for an index of burn severity (difference normalized burn ratio; dNBR) in the Mojave Desert of North America. Predictions were derived from a Random Forest model with 9 variables representing variability in topography, climate, and vegetation.

variables (Balch et al., 2013; Underwood et al., 2019). Second, our focus was on predicting patterns that were integrated over time rather than year-to-year. Had our focus been on year-to-year patterns as in some prior studies (Brooks and Matchett, 2006; Hegeman et al., 2014), then the importance rankings would likely have been higher. Broadly though, this provides a useful example of why interpretation of variable rankings from machine learning models needs to be done carefully and in a meaningful context.

Perhaps the most valuable insight from the variable rankings was that predictions of the models were improved by combined effects of the variables more so than any overriding effects of just one or two of them. Pseudo-R^2 values must be interpreted very cautiously because they are not a measure of explained variance, nor do they range between 0 and 1 (McFadden, 1974). They can be useful for comparing models though, and in this context they gave a clear indication that the most accurate dNBR model included topography, climate, and vegetation variables. The removal of any one variable from the model of probability of ignition did little to change gain in prediction accuracy, and while topography was of minimal importance in the ignition probability and fire frequency models, combined effects of vegetation and climate variables had the greatest effect on prediction accuracy in those models. Moreover, the most important predictor variables in our ignition model compared well with those from a parametric model of ignition probability developed for a limited area of the Mojave (Hegeman et al., 2014). Interpreting our models is best done within a more predictive than explanatory framework, but the predictions were consistent with current understanding of how different environmental factors influence fire in the Mojave (Tagestad et al., 2016; Brooks et al., 2018; Underwood et al., 2019). As a result, they provide the theoretical foundation for parametric models of ignition and severity that have a more explicit explanatory purpose.

Interactions among climate, fuel load, and invasive annual grasses have been a major factor in a large proportion of the Great Basin Desert undergoing conversion from native dominated shrubland to invasive dominated grassland (Whisenant, 1990; Pilliod et al., 2017; Bradley et al., 2018; Chambers et al., 2019). Similar conversions have occurred in the other three North American deserts, but they have not been as extensive or were transient (Klinger and Brooks, 2017). There remains considerable concern though that the other deserts might follow a similar trajectory as the Great Basin (Brooks and Pyke, 2001; Chambers et al., 2019; Fusco et al., 2019). Climate shifts could increase future fire activity, with the magnitude of change likely structured by fuel loads along gradients of elevation and latitude (Abatzaglou and Williams, 2016; Tagestad et al., 2016). However, it is unlikely changes in climate and fuel load alone will bring about large-scale and long-term fire-mediated transformations in the Mojave. Rather, most evidence suggests that invasive annual grasses will be the key factor in these transformations, especially in regard to how ubiquitous the GFC becomes (Balch et al., 2013; Fusco et al., 2019; Underwood et al., 2019). The fire regime and composition of post-fire vegetation are the two fundamental

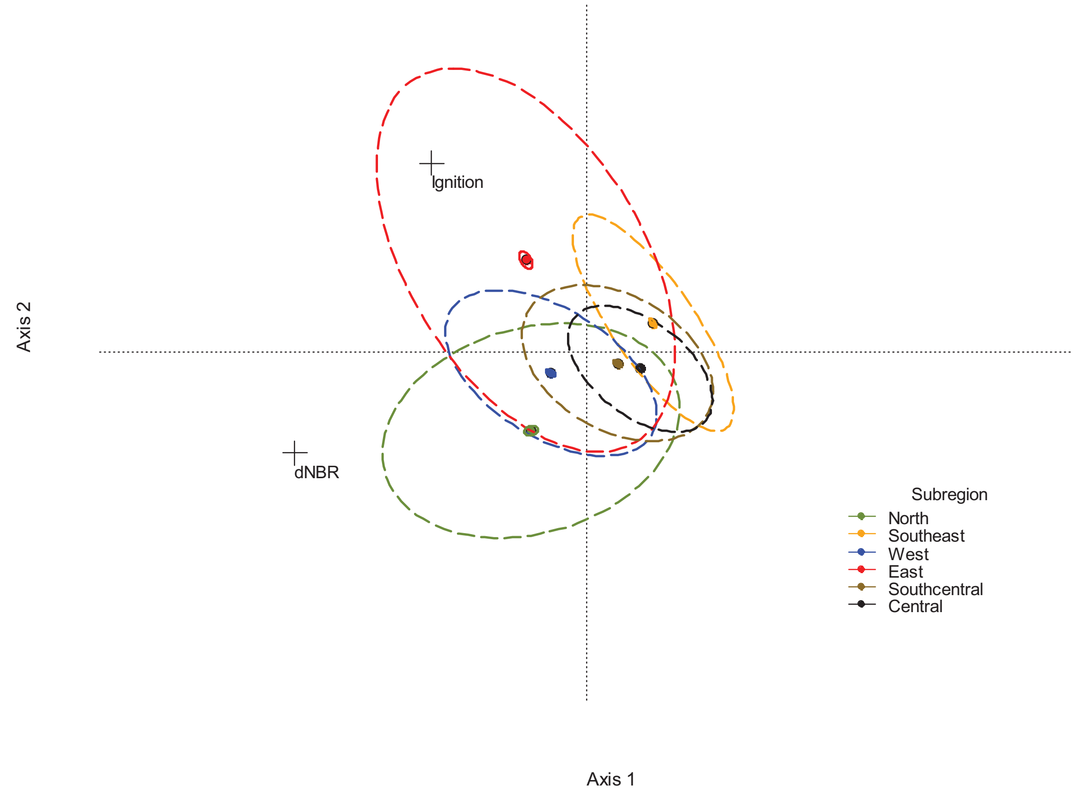

FIGURE 10 | Centroids and ellipses of SEs (solid lines) and 95% confidence bounds (dashed lines) for six subregions of the Mojave Desert along gradients of predicted burn severity (difference normalized burn ratio; dNBR) and probability of ignition. The centroids and ellipses were derived from a Redundancy Analysis with 500 randomly selected points in each subregion from which values of dNBR and ignition probability were extracted. Monte Carlo permutation tests (*N* = 999) and Tukey HSD contrasts indicated the subregions differed in both location (centroids) and dispersion (variance).

components of the GFC, and our findings suggest these can be meaningfully evaluated from two perspectives: their current extent and magnitude and predicted extent and magnitude.

Currently, the proportion of the Mojave that has experienced wildfire over the last 40–50 years is low. In addition, the spatial extent of areas that have experienced multiple wildfires is extremely limited and largely restricted to one part of the region. There is evidence that GFCs have become established in some areas where multiple wildfires occurred (Klinger and Brooks, 2017; Underwood et al., 2019), but our findings indicate they do not occur extensively outside of those areas. Furthermore, even when areas in the Mojave burn two times over several decades and are dominated by invasive grasses in the initial years after burning, this does not mean they will remain so (Klinger and Brooks, 2017). It may take several decades to re-establish, but shrub cover can be resilient, and even if herbaceous cover remains higher than it would if a site was unburned the dominant species may be native (Klinger and Brooks, 2017). When looked at from this viewpoint, a reasonable assessment is the extent and magnitude of changes in fire regimes and post-fire vegetation communities in the Mojave have been limited. Thus, the likelihood of the GFC becoming widespread is low, as is the potential for vegetation communities to undergo extensive, long-term transformations following fire.

A different assessment can be reached when looking at the predicted patterns of probability of ignition, fire frequency, and burn severity. A conspicuous distinction between the actual fire perimeters and predicted pattern of ignition is that there are extensive areas with moderate to high probabilities of ignition where wildfires have not occurred in the last 40–50 years. This is especially apparent in the northern and western parts of the region, including mountain ranges where wildfires have either not occurred or been of very limited extent. The contrast between potential and actual occurrence is also apparent for fire frequency and dNBR; areas predicted to have multiple wildfires are present in most of the interior mountain ranges and large portions of the central, western and northern parts of the region are predicted to have moderate to high burn severity. From a plant community perspective, the predicted frequency and burn severity patterns have important implications. Broader extent of areas that burn multiple times over the course of approximately a half-century undoubtedly means that the GFC would become more prevalent in the Mojave, especially when these areas have favorable habitat conditions for invasive grasses (Underwood et al., 2019). There is virtually no resilience in shrub cover when woody-dominated areas burn more than twice in a half-century (Klinger and Brooks, 2017), hence transformations to invasive-dominated herbaceous communities would become more widespread. In addition,

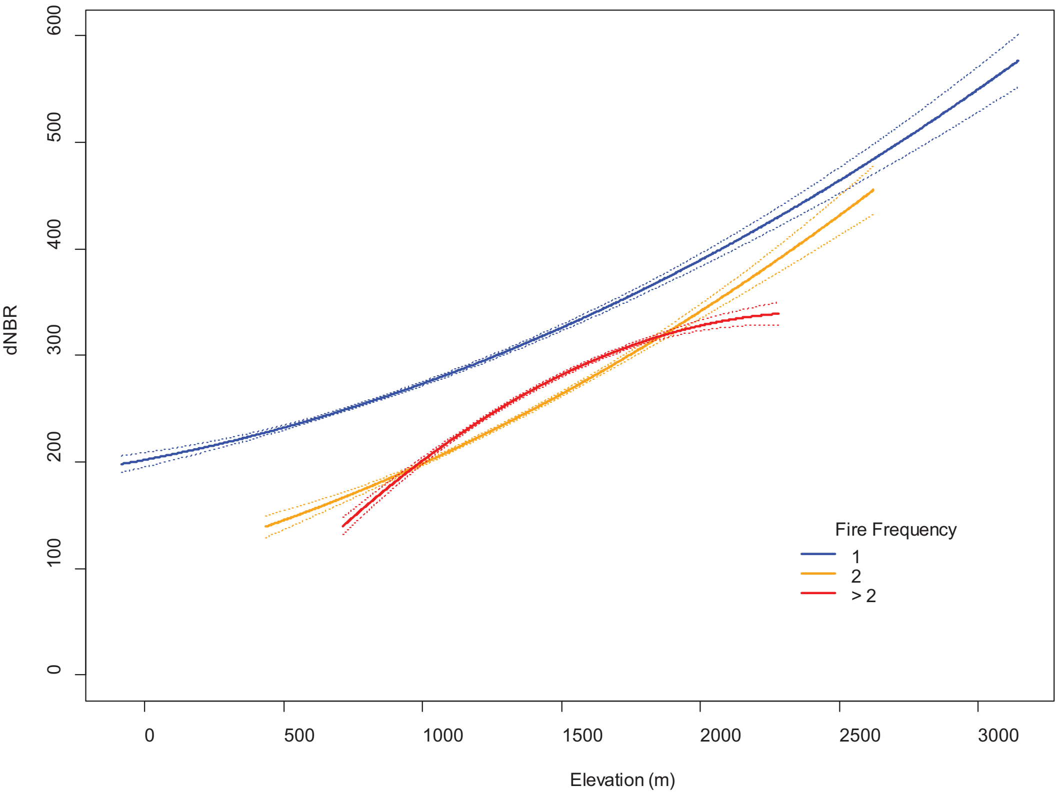

FIGURE 11 | Relationship of predicted values (±95% CI) of burn severity (difference normalized burn ratio; dNBR) and fire frequency (number of times burned from 1972 to 2010) along an elevation gradient in the Mojave Desert of North America. Estimates were derived by ordinary least-squares regression from 1,000 randomly selected points in each fire frequency class.

because woody-dominated communities can be transformed to invasive dominated communities following high or moderate severity burns (Klinger and Brooks, 2017), transitions could occur even when fire is infrequent. Moreover, such areas could act as large-scale nascent foci (Moody and Mack, 1988) from which invasive grasses could spread into adjacent unburned areas. Shifts in precipitation patterns could further contribute to altered fire regimes and plant communities in the next 50–100 years (Tagestad et al., 2016), but widespread changes might occur even sooner. Our findings indicate that conditions for the GFC to become more common already exist, and it is just a matter of time before it does. Moreover, the rate at which this occurs could be greatly exacerbated by human-caused fires (Syphard et al., 2007, 2017; Hegeman et al., 2014; Balch et al., 2017). Thus, based on potential effects, a justifiable assessment would be that the likelihood of the GFC becoming widespread and vegetation communities undergoing extensive, long-term transformations following fire are high.

CONCLUSION

Reconciling the opposing perspectives on the degree to which fire regimes and composition of post-fire vegetation communities in the Mojave might be altered may depend on an interplay between spatial and temporal dynamics of wildfire. Two studies using an ecologically sensible delineation of the Mojave have analyzed the annual number of wildfires and area burned, and both found no evidence of a trend in either variable (Brooks and Matchett, 2006; Klinger et al., unpublished). What was perhaps their most important finding was that relatively few or even no large wildfires (i.e., >405 ha) occurred in most years, but then those periods would be punctuated at 10–15-year intervals by a year ("pulse years") when larger than normal numbers of wildfires and area burned occurred. Moreover, there were uncommon but highly exceptional years when the number of wildfires and amount of area burned were orders of magnitude greater than normal or pulse years ("mega years"). An example of a mega year was 2005, when 25% of the wildfires between 1972 and 2010 occurred and the area burned was 176% that of the total area burned between 1972 and 2004. In addition to the unusually large number of fires and area burned that year, there was a conspicuous spatial pattern of the fires occurring primarily in the eastern part of the region. This suggests a possibility that the distribution of wildfire in the Mojave is temporally dynamic. Areas with disproportionally high fire frequency, occurrence of the GFC, and altered vegetation communities might remain concentrated in a few specific parts of the region for many decades. The pattern could abruptly shift though because of an uncommon but abnormally high magnitude wildfire event in another part of the region. This event would shape trajectories in the structure and composition of post-fire vegetation communities for many decades, with both the GFC and altered communities becoming more prevalent in parts of the region where they had been uncommon for long periods of time. If this dynamic did occur, then the GFC would likely appear to have a limited spatial distribution when viewed over a few decades. But when viewed over many decades or more, the occurrence of the GFC would likely appear more widespread.

DATA AVAILABILITY STATEMENT

Data deposited at USGS (https://doi.org/10.5066/P99YGHSJ).

AUTHOR CONTRIBUTIONS

RK, EU, RM, and MB conceived and designed the study. RM developed the fire atlas. RK developed the PPM and RF models. EU and RK developed the Maxent model. RK wrote the manuscript with contributions from RM, EU, and MB. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.593167/full#supplementary-material

REFERENCES

Abatzaglou, J. T., and Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci. U.S.A.* 113, 11770–11775. doi: 10.1073/pnas.1607171113

Abatzoglou, J. T., and Kolden, C. A. (2011). Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecol. Manag.* 64, 471–478. doi: 10.2111/rem-d-09-00151.1

Abatzoglou, J. T., and Kolden, C. A. (2013). Relationships between climate and macroscale area burned in the western United States. *Inter. J. Wildland Fire* 22, 1003–1020. doi: 10.1071/WF13019

Abella, S. (2010). Disturbance and plant succession in the Mojave and Sonoran deserts of the American Southwest. *Int. J. Environ. Res. Public Health* 7, 1248–1284. doi: 10.3390/ijerph7041248

Alvarez, O., Guo, Q., Klinger, R. C., Li, W., and Doherty, P. (2013). Comparison of elevation and remote sensing derived products as auxiliary data for climate surface interpolation. *Intern. J. Climatol.* 34, 2258–2268. doi: 10.1002/joc.3835

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austr. Ecol.* 26, 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Baddeley, A., Rubak, E., and Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications with R*. London: CRC Press.

Balch, J. K., Bradley, B. A., Abatzoglou, J. T., Nagy, R. C., Fusco, E. J., and Mahood, A. L. (2017). Human-started wildfires expand the fire niche across the United States. *Proc. Natl. Acad. Sci. U.S.A.* 114, 2946–2951. doi: 10.1073/pnas.1617394114

Balch, J. K., Bradley, B. A., D'Antonio, C. M., and Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Glob. Change Biol.* 19, 173–183. doi: 10.1111/gcb.12046

Batllori, E., Parisien, M. A., Krawchuk, M. A., and Moritz, M. A. (2013). Climate change-induced shifts in fire for Mediterranean ecosystems. *Glob. Ecol. Biogeogr.* 22, 1118–1129. doi: 10.1111/geb.12065

Bradley, B. A., Curtis, C. A., Fusco, E. J., Abatzoglou, J. T., Balch, J. K., Dadashi, S., et al. (2018). *Cheatgrass* (*Bromus tectorum*) distribution in the intermountain western United States and its relationship to fire frequency, seasonality, and ignitions. *Biol. Invas.* 20, 1493–1506. doi: 10.1007/s10530-017-1641-8

Breiman, L. (2001). Random forests. *Mach. Learn.* 45, 5–32.

Brooks, M. L. (1999). Alien annual grasses and fire in the Mojave desert. *Madrono* 46, 13–19.

Brooks, M. L., and Berry, K. H. (2006). Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. *J. Arid Environ.* 67, 100–124. doi: 10.1016/j.jaridenv.2006.09.021

Brooks, M. L., and Chambers, J. (2011). Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangeland Ecol. Manag.* 64, 431–438. doi: 10.2111/rem-d-09-00165.1

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., et al. (2004). Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688. doi: 10.1641/0006-3568(2004)054[0677:eoiapo]2.0.co;2

Brooks, M. L., and Esque, T. C. (2002). Alien plants and fire in desert tortoise (*Gopherus agassiz*) habitat of the Mojave and Colorado deserts. *Chelon. Conserv. Biol.* 4, 330–340.

Brooks, M. L., and Matchett, J. R. (2006). Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. *J. Arid Environ.* 67, 148–164. doi: 10.1016/j.jaridenv.2006.09.027

Brooks, M. L., Minnich, R., and Matchett, J. R. (2018). "Southeastern deserts bioregion," in *Fire in California's Ecosystems*, 2nd Edn, eds J. W. Van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. Fites-Kaufman (Berkeley, CA: University of California Press).

Brooks, M. L., and Pyke, D. (2001). "Invasive plants and fire in the deserts of North America," in *Proceedings of the Invasive Species Workshop: The Role of Fire In the Control and Spread of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention and Management*, eds K. Galley and T. Wilson (Tallahassee, FL: Tall Timbers Research Station), 1–14.

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*. Cham: Springer.

Chambers, J. C., Brooks, M. L., Germino, M. J., Maestas, J. D., Board, D. I., Jones, M. O., et al. (2019). Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. *Front. Ecol. Evol.* 7:185. doi: 10.3389/fevo.2019.00185

Chambers, J. C., Roundy, B. A., Blank, R. R., Meyer, S. E., and Whittaker, A. (2007). What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecol. Monogr.* 77, 117–145. doi: 10.1890/05-1991

Collins, B. M., Omi, P. N., and Chapman, P. L. (2006). Regional relationships between climate and wildfire-burned area in the Interior West, USA. *Can. J. For. Res.* 36, 699–709. doi: 10.1139/X05-264

Crisci, C., Ghattasb, B., and Pererac, G. (2012). A review of supervised machine learning algorithms and their applications to ecological data. *Ecol. Model.* 240, 113–122. doi: 10.1016/j.ecolmodel.2012.03.001

Cutler, D. R., Edwards, T. C. J., Beard, K., Cutler, A., Hess, K. T., Gibson, J., et al. (2007). Random forest for classification in ecology. *Ecology* 88, 2783–2792.

D'Antonio, C. M., and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87. doi: 10.1146/annurev.es.23.110192.000431

Dennison, P. E., Brewer, S. C., Arnold, J. D., and Moritz, M. A. (2014). Large wildfire trends in the western United States, 1984-2011. *Geophys. Res. Lett.* 41, 2928–2933. doi: 10.1002/2014GL059576

Dwyer, J. L., Roy, D. P., Sauer, B., Jenkerson, C. B., Zhang, H. K., and Lymburner, L. (2018). Analysis ready data: enabling analysis of the landsat archive. *Remote Sens.* 10:1363. doi: 10.3390/rs10091363

Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., and Howard, S. (2007). A project for monitoring trends in burn severity. *Fire Ecol.* 3, 3–21. doi: 10.4996/fireecology.0301003

Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.

Elith, J., Phillips, S. J., Hastie, T., Dudık, M., Chee, Y. E., and Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distribut.* 17, 43–57. doi: 10.1111/j.1472-4642.2010.00725.x

Forkel, M., Carvalhais, N., Verbesselt, J., Mahecha, M. D., Neigh, C., and Reichstein, M. (2013). Trend change detection in NDVI time series: effects of inter-annual variability and methodology. *Remote Sens.* 5, 2113–2144. doi: 10.3390/rs5052113

Forkel, M., Migliavacca, M., Thonicke, K., Reichstein, M., Schaphoff, S., Weber, U., et al. (2015). Co-dominant water control on global inter-annual variability and trends in land surface phenology and greenness. *Glob. Chang. Biol.* 21, 3414–3435. doi: 10.1111/gcb.12950

Fusco, E. J., Finn, J. T., Balch, J. K., Nagy, R. C., and Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proc. Natl. Acad. Sci. U.S.A.* 116, 23599–23599.

Hegeman, E. E., Dickson, B. G., and Zachmann, L. J. (2014). Probabilistic models of fire occurrence across National Park Service units within the Mojave desert network, USA. *Landscape Ecol.* 29, 1587–1600. doi: 10.1007/s10980-014-0078-z

Hereford, R., Webb, R. H., and Longpre, C. I. (2006). Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893-2001. *J. Arid Environ.* 67, 13–34. doi: 10.1016/j.jaridenv.2006.09.019

Hijmans, R. J. (2012). Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null-model. *Ecology* 93, 679–688. doi: 10.1890/11-0826.1

Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling. R Package Version 3.0-12*. Available online at: https://CRAN.R-project.org/package=raster (accessed May 2020).

Hijmans, R. J., Phillips, S., Leathwick, J., and Elith, J. (2017). *dismo: Species Distribution Modeling. R Package Version 1.1-4*. Available online at: https://CRAN.R-project.org/package=dismo (accessed May 2020).

Hudak, A. T., Morgan, P., Bobbitt, M. J., Smith, A. M. S., Lewis, S. A., Lentile, L. B., et al. (2007). The relationship of multispectral satellite imagery to immediate fire effects. *Fire Ecol.* 31, 64–90. doi: 10.4996/fireecology.0301064

Humphries, G. R. W., Magness, D. R., and Huettmann, F. (2018). *Machine Learning for Ecology and Sustainable Natural Resource Management*. Berlin: Springer.

Key, C. H., and Benson, N. C. (2006). "Landscape Assessment (LA): sampling and analysis methods," in *FIREMON: Fire Effects Monitoring and Inventory System*, eds D. C. Lutes, R. E. Keane, N. C. Caratti, C. H. Key, and S. Sutherland (Fort Collins, CO: Rocky Mountain Research Station), 1–55.

Klinger, R. C., and Brooks, M. L. (2017). Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems. *J. Ecol.* 105, 1521–1533. doi: 10.1111/1365-2745.12863

Klinger, R. C., McKinley, R., and Brooks, M. L. (2019). An evaluation of remotely sensed indices for quantifying burn severity in arid ecoregions. *Intern. J. Wildland Fire* 28, 951–968. doi: 10.1071/wf19025

Legendre, P., and Legendre, L. (1998). *Numerical Ecology*, 2nd Edn, Amsterdam: Elsevier.

Liaw, A., and Wiener, M. (2002). Classification and regression by random forest. *R. News* 2, 18–22.

Littell, J. S., McKenzie, D., Peterson, D. L., and Westerling, A. L. (2009). Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. *Ecol. Appl.* 19, 1003–1021. doi: 10.1890/07-1183.1

Lobo, J. M., Jimenez-Valverde, A., and Real, R. (2007). AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* 17, 145–151. doi: 10.1111/j.1466-8238.2007.00358.x

MacMahon, J. A., and Wagner, F. H. (1985). "The Mojave, Sonoran, and Chihuahuan deserts of North America," in *Hot deserts and Arid Shrublands*, eds M. Evanari, I. Noy-Meir, and D. W. Goodall (Amsterdam: Elsevier), 105–202.

Manly, B. F., McDonald, L., Thomas, D., McDonald, T. L., and Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Berlin: Springer.

Martin, Y., Zuniga-Anton, M., and Mimbreror, M. R. (2019). Modelling temporal variation of fire-occurrence: towards the dynamic prediction of human wildfire ignition danger in northeast Spain. *Geomat. Nat. Hazards Risk* 10, 385–411. doi: 10.1080/19475705.2018.1526219

McFadden, D. (1974). "Conditional logit analysis of qualitative choice behavior," in *Frontiers in Econometrics*, ed. P. Zarembka (Cambridge, MA: Academic Press), 105–142.

Miller, J. D., Skinner, C. N., Safford, H. D., Knapp, E. E., and Ramirez, C. M. (2012). Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecol. Applic.* 22, 184–203. doi: 10.1890/10-2108.1

Moody, M. E., and Mack, R. N. (1988). Controlling the spread of plant invasions: the importance of nascent foci. *J. Appl. Ecol.* 25, 1009–1021. doi: 10.2307/2403762

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2020). *vegan: Community Ecology Package. R Package Version 2.5-7*. Available online at: https://CRAN.R-project.org/package=vegan

Olden, J. D., Lawler, J. J., and Poff, N. L. (2008). Machine learning methods without tears: a primer for ecologists. *Q. Rev. Biol.* 83, 171–193. doi: 10.1086/587826

Overpeck, J. T. (2013). Climate science: the challenge of hot drought. *Nature* 503, 350–351. doi: 10.1038/503350a

Parisien, M.-A., Miller, C., Parks, S. A., DeLancey, E. R., Robinne, F. N., and Flannigan, M. D. (2016). The spatially varying influence of humans on fire probability in North America. *Environ. Res. Lett.* 11:75005.

Parisien, M.-A., and Moritz, M. A. (2009). Environmental controls on the distribution of wildfire at multiple spatial scales. *Ecol. Monogr.* 79, 127–154. doi: 10.1890/07-1289.1

Petorelli, N. (2013). *The Normalized Difference Vegetation Index*. Oxford: Oxford University Press.

Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., and Dudik, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175. doi: 10.1111/j.0906-7590.2008.5203.x

Pilliod, D. S., Welty, J. L., and Arkle, R. S. (2017). Refining the *cheatgrass*-fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. *Ecol. Evol.* 7, 8126–8151. doi: 10.1002/ece3.3414

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Renner, I. W., and Warton, D. I. (2013). Equivalence of MAXENT and poisson point process models for species distribution modeling in ecology. *Biometrics* 69, 274–281. doi: 10.1111/j.1541-0420.2012.01824.x

Richardson, D. M., Pysek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., and West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distribut.* 6, 93–107. doi: 10.1046/j.1472-4642.2000.00083.x

Steel, Z. L., Safford, H. D., and Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6:8.

Syphard, A. D., Keeley, J. E., and Abatzoglou, J. T. (2017). Trends and drivers of fire activity vary across California aridland ecosystems. *J. Arid Environ.* 144, 110–122. doi: 10.1016/j.jaridenv.2017.03.017

Syphard, A. D., Massada, A. B., Butsic, V., and Keeley, J. E. (2013). Land use planning and wildfire: development policies influence future probability of housing loss. *PLoS One* 8:e71708. doi: 10.1371/journal.pone.0071708

Syphard, A. D., Radeloff, V. C., Keeley, J. E., Hawbaker, T. J., Murray, I., Clayton, K., et al. (2007). Human influence on California fire regimes. *Ecol. Appl.* 17, 1388–1402. doi: 10.1890/06-1128.1

Tagestad, J., Brooks, M. L., Cullinan, V., Downs, J., and McKinley, R. (2016). Precipitation regime classification for the Mojave desert: implications for fire occurrence. *J. Arid Environ.* 124, 388–397. doi: 10.1016/j.jaridenv.2015.09.002

Underwood, E. C., Klinger, R. C., and Brooks, M. L. (2019). Effects of invasive plants on fire regimes and post-fire vegetation diversity in an arid ecosystem. *Ecol. Evol.* 9, 1–15. doi: 10.1002/ece3.5650

Webb, R. H., Fenstermaker, L. F., Heaton, J. S., Hughson, D. L., McDonald, E. V., and Miller, D. M. (eds) (2009). *The Mojave Desert: Ecosystem Processes and Sustainability*. Reno, NV: University of Nevada Press.

Westerling, A. L., Brown, T. J., Gershunov, A., Cayan, D. R., and Dettinger, M. D. (2003). Climate and wildfire in the western United States. *Bull. Am. Meteorol. Soc.* 84, 595–604. doi: 10.1175/BAMS-84-5-595

Westerling, A. L., Hidalgo, H. G., Cayan, D. R., and Swetnam, T. W. (2006). Warming and earlier spring increases western US forest wildfire activity. *Science* 313, 940–943. doi: 10.1126/SCIENCE.1128834

Whisenant, S. G. (1990). "Changing fire frequencies on Idaho's Snake River plains: Ecological and management implications," in *Proceedings of the Symposium Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management, General Technical Report INT 276*, eds E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller (Ogden, UT: US Department of Agriculture), 4–10.

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., and Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Mar. Geodesy* 30, 3–35. doi: 10.1080/01490410701295962

Wright, H. A., and Bailey, A. W. (1982). *Fire Ecology: United States and Southern Canada*. New York, NY: John Wiley and Sons, Inc.

Zhu, Z., Key, C., Ohlen, D., and Benson, N. (2006). *Evaluate Sensitivities of Burn-Severity Mapping Algorithms for Different Ecosystems and Fire Histories in the United States*. Final Report to the Joint Fire Science Program, Project: JFSP 01-1-4-12. Sioux Falls, SD: USGS EROS.

Zouhar, K., Kapler-Smith, J., Sutherland, S., and Brooks, M. L. (2008). *Wildland Fire in Ecosystems: Fire And Nonnative Invasive Plants*. General Technical Report, RMRS-GTR-42, Vol. 6. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 355.

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REVIEW
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Fire and Its Interactions With Other Drivers Shape a Distinctive, Semi-Arid 'Mallee' Ecosystem

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Fire shapes ecosystems globally, including semi-arid ecosystems. In Australia, semi-arid 'mallee' ecosystems occur primarily across the southern part of the continent, forming an interface between the arid interior and temperate south. Mallee vegetation is characterized by short, multi-stemmed eucalypts that grow from a basal lignotuber. Fire shapes the structure and functioning of mallee ecosystems. Using the Murray Mallee region in south-eastern Australia as a case study, we examine the characteristics and role of fire, the consequences for biota, and the interaction of fire with other drivers. Wildfires in mallee ecosystems typically are large (1000s ha), burn with high severity, commonly cause top-kill of eucalypts, and create coarse-grained mosaics at a regional scale. Wildfires can occur in late spring and summer in both dry and wet years. Recovery of plant and animal communities is predictable and slow, with regeneration of eucalypts and many habitat components extending over decades. Time since the last fire strongly influences the distribution and abundance of many species and the structure of plant and animal communities. Animal species display a discrete set of generalized responses to time since fire. Systematic field studies and modeling are beginning to reveal how spatial variation in fire regimes ('pyrodiversity') at different scales shapes biodiversity. Pyrodiversity includes variation in the extent of post-fire habitats, the diversity of post-fire age-classes and their configuration. At regional scales, a desirable mix of fire histories for biodiversity conservation includes a combination of early, mid and late post-fire age-classes, weighted toward later seral stages that provide critical habitat for threatened species. Biodiversity is also influenced by interactions between fire and other drivers, including land clearing, rainfall, herbivory and predation. Extensive clearing for agriculture has altered the nature and impact of fire, and facilitated invasion by pest species that modify fuels, fire regimes and post-fire recovery. Given the natural and anthropogenic drivers of fire and the consequences of their interactions, we highlight opportunities for conserving mallee ecosystems. These include learning from and fostering Indigenous knowledge of fire, implementing actions that consider synergies between fire and other processes, and strategic monitoring of fire, biodiversity and other drivers to guide place-based, adaptive management under climate change.

Keywords: fire regimes, mallee, biodiversity, species responses to fire, pyrodiversity

INTRODUCTION

Fire shapes ecosystems worldwide (He et al., 2019; Kelly et al., 2020). Over half of Earth's land surface is affected by fire, and some 30% experiences frequent fire (Chuvieco et al., 2008). There is increasing recognition of the role of fire as a major ecological and evolutionary force that has influenced global patterns of biodiversity, including the composition and structure of vegetation, species richness at local and landscape scales, levels of endemism and functional traits of plant and animal communities (He et al., 2019). Human activity and anthropogenic drivers (e.g., land use, biotic invasions, climate change) increasingly are transforming fire activity, with at least 4,400 species from a wide range of taxa and habitats facing threats associated with changing patterns of fire (Kelly et al., 2020). Importantly, fire does not occur in a uniform manner; rather, fire regimes – including the size, severity, frequency, season, extent and patchiness of fires – differ in distinctive ways between ecosystems (Chuvieco et al., 2008; Archibald et al., 2013). Consequently, for fire-prone ecosystems worldwide, understanding the role of fire in ecosystem function is critical for guiding future conservation and management.

Arid and semi-arid ecosystems make up a substantial component of the global area influenced by fire (Archibald et al., 2013). In Australia, arid ecosystems occupy ∼70% of the interior of the continent and encompass a range of vegetation types: *Acacia* woodlands, eucalypt woodlands, chenopod shrublands, hummock grasslands and tussock grasslands (Morton et al., 2011). To the north, driven by increasing and regular seasonal rainfall, arid ecosystems transition into tropical savannah woodlands and grasslands; to the south, they give way to semi-arid woodlands and shrublands. 'Mallee' vegetation - a major component of southern semi-arid woodlands - is a distinctive fire-prone ecosystem and the focus of this review. This ecosystem is dominated by evergreen sclerophyllous woodlands and shrublands that become highly flammable in dry summer months after the winter-spring growing season (Bradstock and Cohn, 2002), a pattern shared with other regions globally including the Mediterranean Basin, central and southern California, central Chile, and the Western Cape province, South Africa (Keeley et al., 2012).

'Mallee' is a colloquial term of Indigenous origin (Noble and Kimber, 1997; Yates et al., 2017), used to describe *Eucalyptus* species with a growth form of two or more stems of similar age arising from a subterranean lignotuber. Mallee eucalypts typically occur as a short (2–8 m) tree or tall shrub (Hill, 1989). The term also refers to a vegetation type, 'mallee vegetation,' dominated by an overstorey of mallee eucalypts. Mallee vegetation occurs at a continental scale across southern Australia, extending from south-western Western Australia to South Australia, Victoria and central New South Wales (**Figure 1**). At the time of European colonization, mallee vegetation probably covered around 302,000 km^2. Since the mid-19th century, approximately one third of mallee vegetation has been cleared, principally for cereal cropping (**Figure 1**). Mallee ecosystems support a diverse flora and fauna, including numerous threatened species, such that effective conservation of this distinctive ecosystem has a key role in maintaining Australian biodiversity (Noble and Bradstock, 1989; Noble et al., 1990).

Understanding the nature, characteristics and role of fire is crucial for conserving mallee biodiversity and responding to threats posed by anthropogenic change. Here, we review the context and role of fire in this semi-arid system, with particular reference to a case-study region in the Murray-Darling Depression Bioregion in south-eastern Australia (**Figure 1**), hereafter referred to as the 'Murray Mallee region.' We first set the context by outlining the landform and soils, climate, broad vegetation patterns, fauna, and human land use of this region. We then address four main questions. (1) What are the patterns and characteristic features of fire in semi-arid mallee ecosystems? (2) How do fire regimes shape biodiversity in this ecosystem? (3) How does fire interact with other drivers to influence biodiversity? (4) What are the potential consequences of a changing climate for fire regimes and their interactions with other drivers? We conclude with a summary of key issues for future conservation of mallee ecosystems and their biota and identify research questions to inform future management.

THE MURRAY MALLEE REGION, SOUTH-EASTERN AUSTRALIA

Extensive tracts of mallee vegetation occur in several regions of southern Australia (**Figure 1**), notably: (a) the Murray Mallee region, encompassing adjoining areas in north-western Victoria, South Australia and western NSW; (b) the Eyre Peninsula and westward in southern South Australia; and (c) semi-arid parts of southern West Australia. While having a similar climate, mallee vegetation in western and south-eastern Australia have been geographically separated since the mid-Tertiary (Hill, 1989), and each has evolved a distinctive flora and fauna (Gosper et al., 2012a; Yates et al., 2017). Here, we focus on the Murray Mallee region (**Figure 2**), while also drawing on research from other mallee ecosystems in southern Australia.

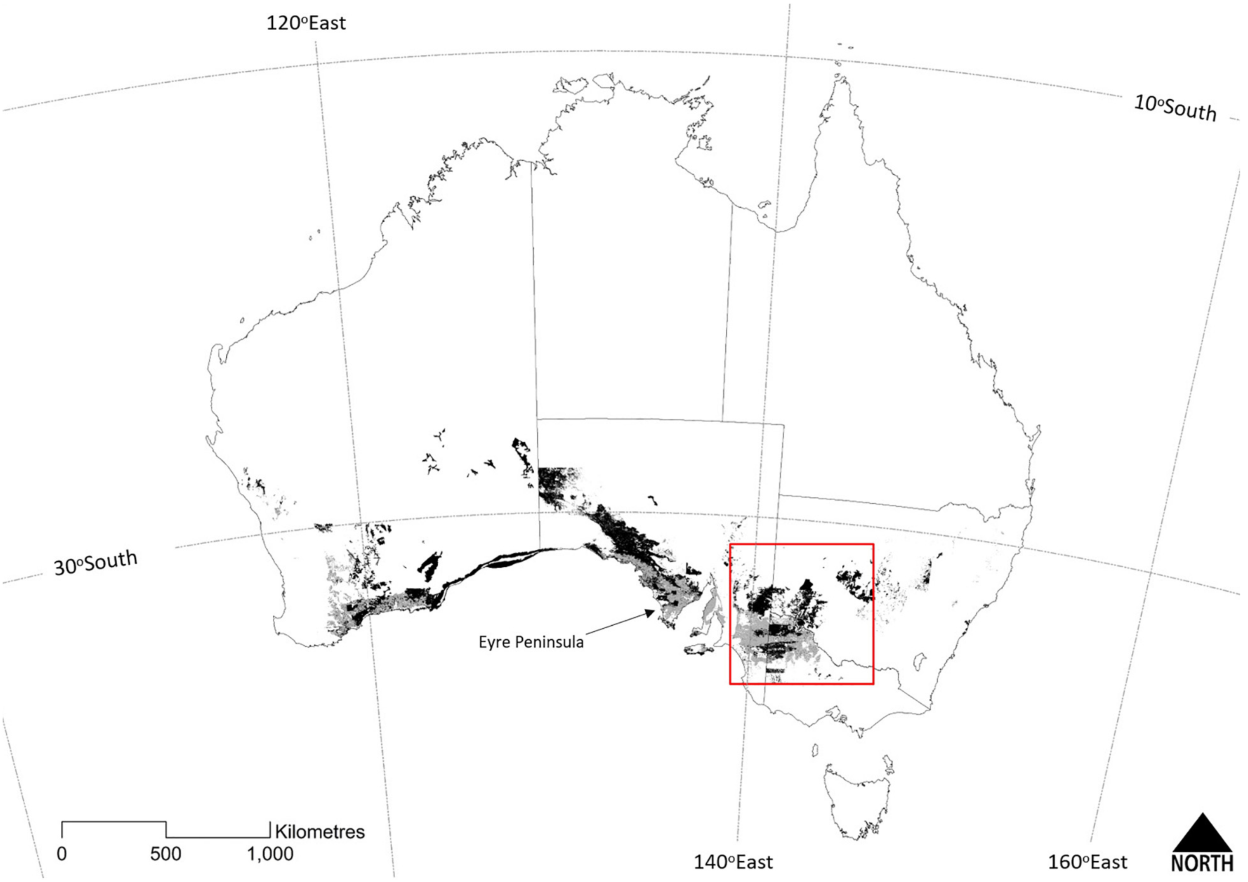

FIGURE 1 | The temperate continental distribution of the Major Vegetation Group 'mallee woodlands and shrublands' across Australia (from Department of the Environment, 2018). Dark shading depicts extant vegetation and lighter shading depicts the likely former extent prior to clearing for agriculture. The red box frames the study area, the Murray-Darling Depression Bioregion (see **Figure 2**). Discontinuities in the extent of mallee vegetation across State borders reflects some inconsistencies between jurisdictional typologies.

Landform and Soils

The topography of the Murray Mallee region is predominantly flat, with modest local differences in elevation (∼20 m) primarily associated with dune systems and lunettes. At a regional scale, the landscape is broken up by saline flats and lakes (boinkas), which is more pronounced in mallee ecosystems in West Australia (O'Donnell et al., 2011a,b). Aside from the river and floodplain systems of the Murray and Darling Rivers, there are few large bodies of fresh surface water. Ephemeral water may pool in clay pans and depressions following heavy rains.

Mallee vegetation is largely restricted to aeolian landforms in the Murray Mallee region (typically dunes, interdunal swales and sandplains) within a broader mosaic interspersed with red earths, ephemeral lakes and lunettes that support very different vegetation communities, e.g., *Allocasuarina* woodlands and chenopod shrublands (Wasson, 1989). The region has two main aeolian formations, the Lowan Sands and the Woorinen Formation (Bowler and Magee, 1978; Pell et al., 2001). The Lowan Sands consists of west-south-west facing dunes; sediments are siliceous with very small quantities of clay and carbonate (Wasson, 1989). Dune systems of the Woorinen Formation comprise closely spaced east-west dunes, that are typically calcareous, and soils are heavier and finer textured than the Lowan Sands (Wasson, 1989).

Soil properties, especially texture and depth, affect the growth and distribution of overstorey *Eucalyptus* species (Parsons and Rowan, 1968; Sparrow, 1989; White, 2006; Pollock et al., 2018) and the composition of understorey species (Cohn et al., 2002; Haslem et al., 2010). This, in turn, influences the local rate of litter accumulation (Travers and Eldridge, 2013) and the flammability of vegetation (Bradstock and Cohn, 2002). Soil fertility is greater, and plant water availability is lower, where there is more clay in the soil (Parsons and Rowan, 1968). The combination of soil properties and flat topography in the Murray Mallee region create few moisture or edaphic barriers, allowing fire to spread rapidly whenever wind speed is sufficient to allow fire spread or ephemeral grasses comprise a well-connected fuel layer.

Climate

The region is semi-arid with cool winters and hot summers. The mean daily maximum temperature in summer months (January and February) exceeds 30°C and daily maxima >40°C

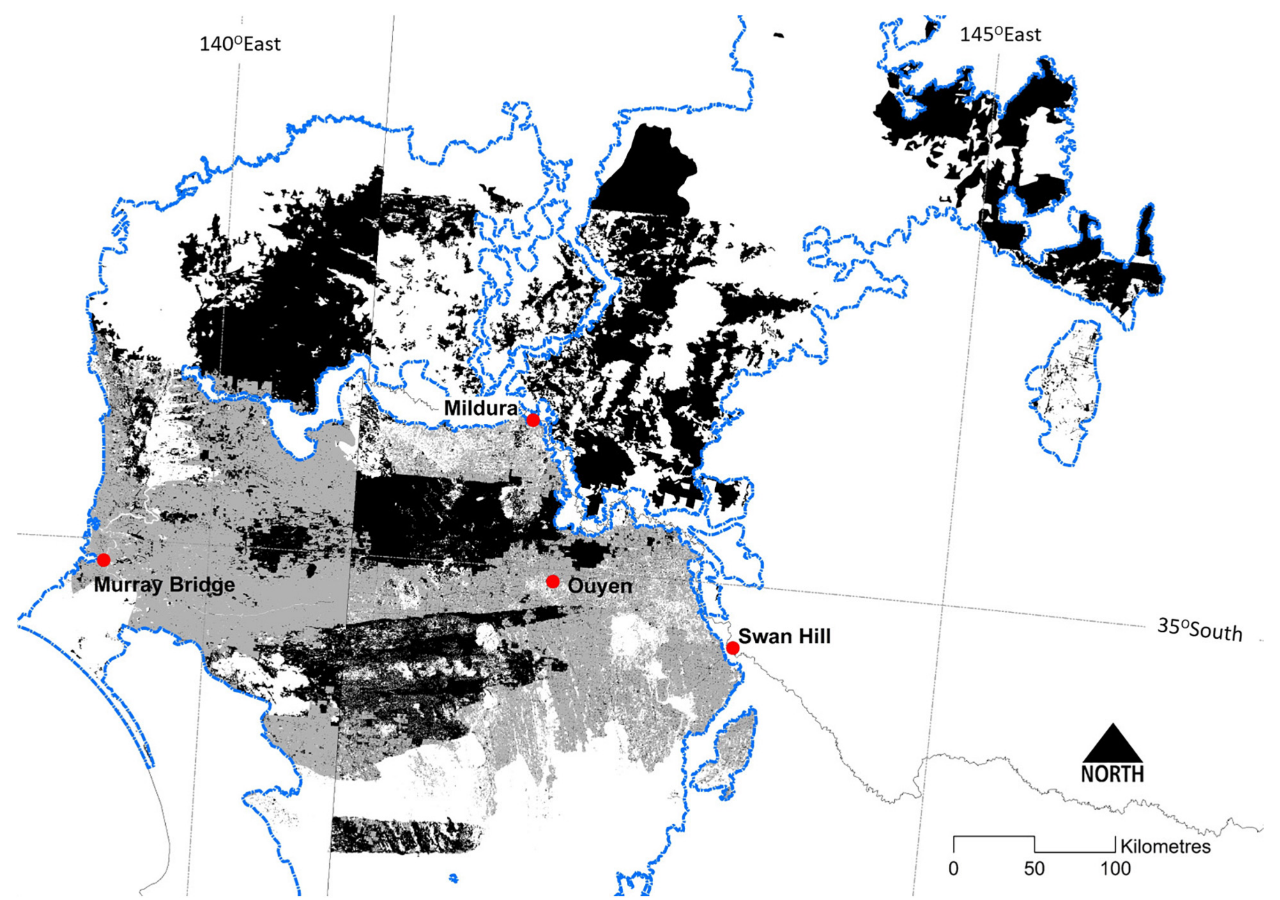

FIGURE 2 | The distribution of the Major Vegetation Group 'mallee woodlands and shrublands' (Department of the Environment, 2018) within the Murray-Darling Depression Bioregion (Department of Sustainability Environment Water Population and Communities, 2013: the 'Murray Mallee region' in this review) (outlined in blue). Dark shading depicts extant vegetation and lighter shading depicts the likely former extent prior to clearing for agriculture. Discontinuities in the extent of mallee vegetation across State borders reflects some inconsistencies between jurisdictional typologies for vegetation.

are common (White, 2006). In winter, minimum temperatures can fall below 0°C overnight, with frequent frosts between May and September (White, 2006).

Mean annual rainfall ranges from ∼250 mm in the north to ∼500 mm in the south (White, 2006). In Australia, arid ecosystems experience rainfall that on a global scale is spatially and temporally unpredictable, such that large, infrequent rain events have a key role in shaping ecosystems (Morton et al., 2011). In contrast, semi-arid mallee ecosystems generally have more predictable and less-variable rainfall than the arid interior. Prolonged periods of below-average rainfall may still occur, as well as periods of high rainfall (White, 2006; Cullen and Grierson, 2009).

Vegetation

Mallee vegetation of the Murray Mallee region reflects variation in topography, soil texture, moisture availability and the long history of fire (Bradstock, 1989a; Cheal and Parkes, 1989; Hill, 1989; Parkes and Cheal, 1990; White, 2006; Cheal, 2010). Common plant families, apart from the Myrtaceae to which the eucalypts belong, include shrubs in the Fabaceae, Euphorbiaceae, Asteraceae, Proteaceae, Chenopodiaceae, Myoporaceae, and Cupressaceae (Bradstock and Cohn, 2002; Yates et al., 2017). While locally mediated by edaphic factors, the composition of the vegetation (e.g., life-form types) and fuel attributes (biomass, dryness and contiguity of fuels) correspond broadly with the north-south gradient in rainfall (Pausas and Bradstock, 2007; Gibson et al., 2014). There is a transition from greater cover of woody sclerophyllous shrubs in higher rainfall areas with sandy soils in the south, to a higher cover of the widespread and distinctive hummock grass *Triodia scariosa* in lower rainfall areas on fine textured clay-rich soils in the north (Gibson et al., 2014).

Here, we outline three broad vegetation types, Triodia Mallee, Chenopod Mallee and Heathy Mallee (Haslem et al., 2010; Yates et al., 2017) as a framework for describing mallee vegetation patterns and, subsequently, faunal patterns and fire responses.

Triodia Mallee represents plant communities on sandy flats and low dunes where the overstorey is dominated by eucalypts (including *Eucalyptus dumosa* and *E. socialis*) and the understorey typically is dominated by the perennial hummock grass *Triodia scariosa* (**Figure 3A**). Triodia Mallee

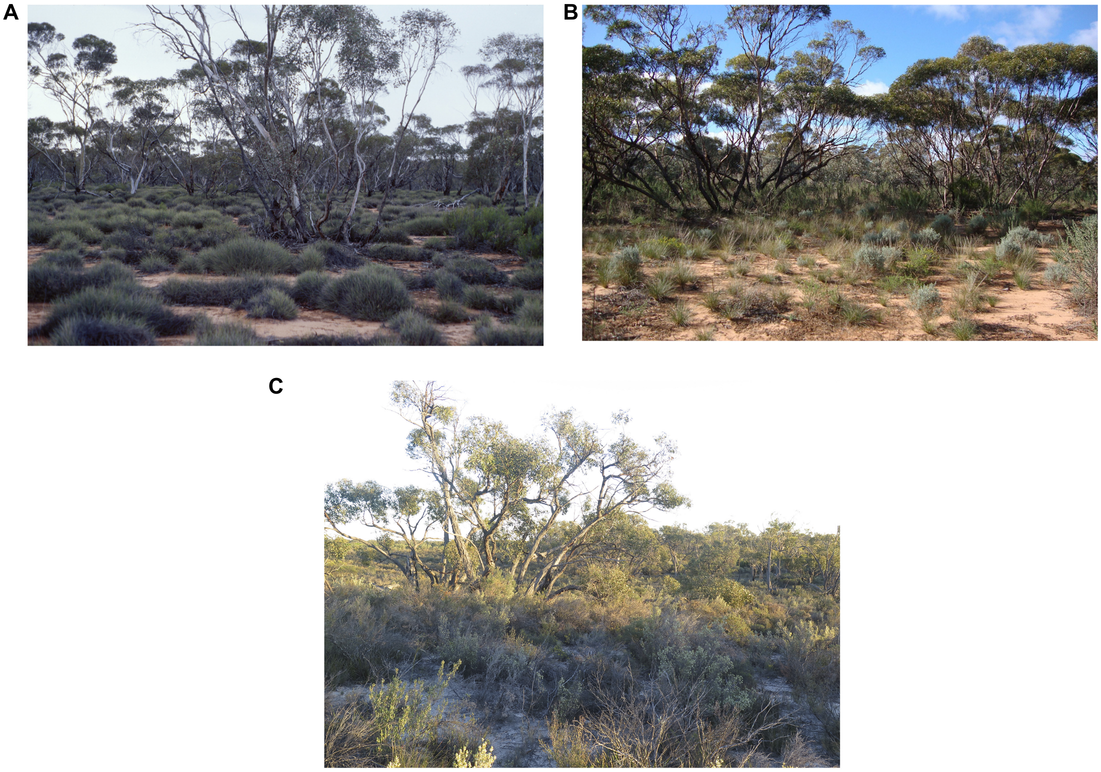

FIGURE 3 | Examples of three broad types of mallee vegetation: **(A)** Triodia Mallee, **(B)** Chenopod Mallee, and **(C)** Heathy Mallee.

is widespread across the region (Haslem et al., 2010) and fire-prone (Avitabile et al., 2013). *Triodia* hummocks are an important structural habitat component for a range of faunal species (Verdon et al., 2020), partly due to their amelioration of environmental temperature (Bell et al., 2021), but they are also a source of fuel for fire (Haslem et al., 2010).

Chenopod Mallee vegetation commonly occurs on heavier-textured soils, notably the swales of the dune fields of the Woorinen Formation. Dominant eucalypt species include *E. oleosa* and *E. gracilis*, with an open understorey of low, perennial chenopod shrubs (e.g., *Maireana*, *Sclerolaena*, and *Atriplex* spp.) (**Figure 3B**). This vegetation type has a lower contiguity of ground-layer fuels and is less fire-prone; much of the long-unburnt mallee vegetation (e.g., > 80 years since last fire) in the region is Chenopod Mallee.

Heathy Mallee vegetation occurs in the southern parts of the region where higher rainfall occurs, on deep aeolian sands (e.g., Big Desert, Little Desert, Ngarkat). It typically comprises sparse mallee eucalypts (e.g., *E. costata*, *E. leptophylla*, and *E. arenacea*) with a diverse understorey of sclerophyllous heathy shrubs (**Figure 3C**). On deep sands, it may give way to treeless heathlands lacking a mallee overstorey, or in places to a tree layer of desert stringybark (*E. arenacea*). The understorey is structurally and floristically diverse and includes numerous shrubs from the genera *Banksia*, *Grevillea*, *Hakea*, *Leptospermum*, and *Melaleuca*. The flowering patterns of these taxa provide a seasonal supply of nectar and seeds for fauna in many years.

Fauna

The fauna of mallee ecosystems reflects the biogeographic context, occupying a transition zone between arid and temperate biomes. The vertebrate fauna (particularly birds) includes representation of both Bassian (temperate) and Eyrean (arid) biogeographic elements, as well as species that occur throughout Australia (Menkhorst and Bennett, 1990).

Mallee ecosystems support distinct faunal communities (Schodde, 1981; Cogger, 1989; Menkhorst and Bennett, 1990), but few species are entirely dependent on mallee vegetation. Most species overlap in occurrence with an adjacent vegetation type (e.g., dryland and temperate woodlands, chenopod shrublands, heathlands). The only vertebrate taxa totally dependent on mallee vegetation are: four passerine birds, the white-bellied whipbird (*Psophodes leucogaster leucogaster*) (Burbidge et al., 2017), red-lored whistler (*Pachycephala rufogularis)*, mallee emu-wren (*Stipiturus mallee*) and black-eared miner (*Manorina melanotis*); one reptile, the eared worm lizard (*Aprasia aurita*); and a small marsupial, the mallee ningaui (*Ningaui yvonneae*) (Menkhorst and Bennett, 1990).

The native mammal fauna of the Murray Mallee region at the time of European colonization (~1840) was diverse; at least 43 species occurred in mallee vegetation (Bennett et al., 1989). Prominent components included members of the families Dasyuridae (marsupial carnivores), Peramelidae (bandicoots), Macropodidae (kangaroos and wallabies), Muridae (native rodents) and Vespertilionidae (insectivorous bats). Rapid and dramatic decline followed, with at least 13 species no longer present including five species now globally extinct (e.g., pig-footed bandicoot *Chaeropus ecaudatus*). Medium-sized species in the critical weight range 0.2–5 kg were most severely affected (Bennett et al., 1989), including ecosystem engineers (e.g., bandicoots, bettongs, and bilbies) that influence water infiltration and nutrient turnover through excavation of soils when foraging or burrowing (Eldridge and James, 2009). This regional loss of mammals was associated with massive changes to the vegetation (~1860–1920) through grazing of domestic stock, introduction and over-abundance of the European rabbit (*Oryctolagus cuniculus*), and severe drought; accompanied by the introduction of exotic predators (red fox *Vulpes vulpes*, cat *Felis catus*) (Bennett et al., 1989, 2006).

Bird communities of mallee ecosystems in southern Australia comprise >150 species, dominated by insectivorous and nectarivorous passerines, with strong representation by parrots and raptors. They comprise taxa associated with arid Australia, melded with species from more-mesic zones (Schodde, 1990; Schodde and Mason, 1999). For example, in the widespread family Meliphagidae (honeyeaters), the white-eared honeyeater (*Nesoptilotis leucotis*), typical of mesic habitats, occurs alongside the yellow-plumed honeyeater (*Ptilotula ornata*) and grey-fronted honeyeater (*Ptilotula plumula*) associated with arid and semi-arid environments. The region also supports taxa that are widespread but exist as 'isolated' populations. For example, the striated grasswren (*Amytornis striatus*) occurs through much of arid Australia, but the isolated population in the region is a distinct subspecies (*A. s. howei*; Black et al., 2020). Similarly, the regent parrot (*Polytelis anthopeplus monarchoides*) is a locally isolated subspecies with a conspecific subspecies in south-western Western Australia.

Reptiles are a prominent component of the vertebrate fauna of mallee ecosystems (Cogger, 1989). A wide range of taxa occur including geckos (Families Gekkonidae, Carphodactylidae, and Diplodactylidae), legless lizards (Pygopodidae), skinks (Scincidae), dragons (Agamidae), goannas (Varanidae), blind snakes (Typhlopidae), python (Pythonidae) and venomous snakes (Elapidae). A relatively high richness of reptiles, both at individual sites and the regional scale, is characteristic of desert ecosystems in Australia (Pianka, 1969). Compositionally, the reptile fauna of mallee vegetation is more similar to that of the arid Eyrean biogeographic region than the mesic Bassian. Geckos, dragons and skinks dominate mallee assemblages, and genera such as *Ctenotus*, *Lerista*, and *Diplodactylus* that have speciated widely in arid environments are prominent in mallee vegetation (Menkhorst and Bennett, 1990).

While the number of frog species in mallee ecosystems is low, several species have adaptations that enable them to persist in this dry environment. In the Murray Mallee region, three species from the family Myobatrachidae occur in mallee vegetation (Menkhorst and Bennett, 1990). Of these, species from the genus *Neobatrachus* are most distinctively associated with mallee vegetation. They avoid desiccation by burrowing into the sandy soil, emerging to feed and breed in suitable conditions, typically following heavy rains.

The invertebrate fauna of mallee ecosystems is diverse, particularly ants (Andersen, 1982, 1983), beetles (Driscoll and Weir, 2005) and predatory arthropods – spiders, scorpions. Termites are widespread and ubiquitous and play a keystone role as herbivores and detritivores (Avitabile et al., 2015). The biogeography of invertebrates in mallee ecosystems is poorly documented, and the relatively few ecological studies of invertebrates in mallee communities relate mainly to responses to fire or land clearing (Andersen and Yen, 1985; Gullan et al., 1997; Schlesinger et al., 1997; Driscoll and Weir, 2005; Driscoll et al., 2020).

Human Land Use

Humans have lived in the Murray Mallee region for tens of thousands of years. The earliest archeological evidence comes from Lake Mungo and dates from 50 to 45,000 years before present (Ross, 1981; Bowler et al., 2003; Richards et al., 2007). The Murray Mallee region is home to Indigenous peoples who have maintained continuous connections to the land. The traditional homeland of some Indigenous peoples centered on river systems and lakes (e.g., Murray and Darling Rivers), with use of mallee vegetation along well-established paths (Clarke, 2009; Burch, 2020). The traditional homeland of other groups, such as the Ngarkat, included the extensive tracts of mallee vegetation (Clarke, 2009) where water was accessed from the roots of mallee trees and by building wells (Noble and Kimber, 1997; Barengi Gadjin Land Council, 2017). A wide range of plants and animals were used for food, medicine, ceremonies and trade. Kangaroos and smaller animals, such as stick-nest rats (*Leporillus* spp.), were hunted for food, and malleefowl (*Leipoa ocellata*) eggs were collected in some areas (Clarke, 2009).

Prior to European colonization, Indigenous peoples across Australia used cultural burning for a wide range of purposes including maintaining travel routes, promoting habitat for animals, harvesting of resources, ceremonies and supporting human health and well-being (e.g., Prober et al., 2016; Bliege Bird and Nimmo, 2018). Indigenous use of fire is a socially and ecologically complex practice, and knowledge is passed generationally within the context of a living culture (Victorian Traditional Owner Cultural Fire Knowledge and Group, 2019). Indigenous fire practices largely ceased in the Murray Mallee region following colonization and there is little written information about the extent and timing of Indigenous use of fire. However, there is emerging attention to traditional fire practices across south-eastern Australia (Smith et al., 2021).

A common theme of Indigenous use of fire is the importance of place-based knowledge; that is, including site-specific knowledge of a locality, its history, fire and fuel characteristics and likely impact on biota. For example, in mallee landscapes in Western Australia, the Ngadju people show how use of fire was tailored to particular locations and vegetation types: frequent fire was applied in some areas and others experienced far less fire (Prober et al., 2016). Intimate knowledge of plants and animals guided cultural burning: for example, prior to low severity burning, local areas were checked for important food plants (e.g., fruit trees), animals (e.g., malleefowl nests) and habitat (e.g., logs) (Prober et al., 2016). A link between anthropogenic fire and future fire risk was evident, with Ngadju emphasizing the importance of burning spinifex surrounding important assets (large, old mallee trees) to ensure they were not lost to wildfire (Prober et al., 2016).

Europeans commenced agriculture in the Murray Mallee region in the 1840s, initially by pastoral occupation (Broome et al., 2020). Traditional land-use practices of Indigenous peoples were rapidly curtailed as people were displaced from traditional lands through killing, disease and assimilation policies (Clarke, 2009). Widespread clearing of mallee vegetation commenced in the 1890s, and especially after World War I via soldier settlement schemes to cultivate land for cereal cropping, primarily south of the Murray River (**Figure 2**). Clearing targeted the most fertile soils; the large blocks of mallee vegetation remaining today (most in conservation reserves, **Figure 4**) are on less-fertile soils. Clearing of mallee vegetation and destruction of cryptogamic soil crusts through trampling by stock left soils vulnerable to wind erosion, and massive dust storms (e.g., in the 1930s) resulted in loss of valuable topsoil. Farm dams were excavated and created more reliable sources of water for stock and wildlife, but grazing pressure around such points exacerbated vegetation change and loss of topsoil (James et al., 1999). Clearing and fragmentation of vegetation, fire suppression, and introduction of planned burning have all contributed to changes in fire regimes.

NATURAL AND ANTHROPOGENIC DRIVERS OF FIRE REGIMES

Patterns and Characteristics of Fire in Mallee Ecosystems

The characteristic features of wildfire in mallee ecosystems (**Table 1**) differ from those in other ecosystems such as temperate forests, tropical savannah or arid hummock grasslands, resulting in more uniform burn severity. This leads to extensive portions of very large fire scars (>10,000 ha) sharing a synchronized stage of recovery post fire. Fires in other ecosystems (e.g., temperate forests) typically encounter more barriers to fire spread, both horizontally and vertically, resulting in greater heterogeneity across the post-fire landscape.

Mallee vegetation is highly flammable, and in the Murray Mallee region wildfires can occur in any given year (Bradstock and Cohn, 2002). Rainfall is sufficiently reliable to sustain perennial plants as a fuel source, and dry, hot conditions in summer months increase the probability that vegetation will carry fire ignited by lightning strikes. Wildfires in southwestern Australian mallee tend to be linked to hot and dry conditions, with few or no fires in cool and wet summers (O'Donnell et al., 2011a, 2014).

Leaf and bark litter are key components of fuel in fires in mallee ecosystems (Bradstock and Gill, 1993). The distribution and abundance of litter contributes to the contiguity of fuels between trees and shrubs (McCaw, 1997). Surface fuels often consist of large 'halos' of shed bark and leaf litter around each mallee tree, with less fuel between halos. Wind is required for fire to spread between patches of fuel. Without strong wind, fire spread in mallee vegetation, even on hot and dry days, is limited (Cruz et al., 2013). This may partly explain the dominance of large fires in mallee ecosystems (**Figure 5**); once the fire-spread threshold is overcome, fires spread rapidly. The spatial patchiness of fuels in mallee vegetation increases from south to north with decreasing rainfall (Pausas and Bradstock, 2007; Gibson et al., 2014). Litter (e.g., depth, cover) does not accumulate in a continuous manner over time, but peaks at ∼20–30 years post-fire and then remains at a plateau or subsequently declines with time (Haslem et al., 2011). Ecosystem engineers, such as fossorial mammals (Hayward et al., 2016), termites and the malleefowl remove litter and consume or bury it, thereby reducing fuel contiguity in ways that can have a measurable impact on fire behavior (Smith et al., 2017).

Wildfires typically are large (**Figure 5**), often the result of multiple, lightning-triggered ignitions merging during a single storm event. Systematic mapping of fire using Landsat imagery for a 100,000 km^2 study area in the northern Murray Mallee region provided a detailed understanding of contemporary fire history (1972–2007) (Avitabile et al., 2013). Large fires (>10,000 ha) occurred regularly (e.g., 16 between 1972 and 2007), with very large fires (>100,000 ha) occurring every 10–20 years; sometimes following drought and sometimes major rainfall events (as is also seen in West Australian mallee, O'Donnell et al., 2011b, 2014). Smaller fires (<10,000 ha, generally <100 ha) occur every year. Over this 35-year period, an area equivalent to 40% of mallee vegetation in the study area was burnt, of which large fires (>10,000 ha) were responsible for more than 89% of the area burnt.

The interval between wildfires can be long, due to the slow rate of fuel recovery (O'Donnell et al., 2014). Chenopod and Triodia Mallee vegetation are capable of carrying a fire 10–20 years after the previous fire; much sooner (within 2 years) if high rainfall has stimulated widespread growth of ephemeral grasses (Noble and Vines, 1993; O'Donnell et al., 2011a, 2014). Heathy Mallee vegetation can burn in less than 10 years after a previous wildfire, as is evident in the higher fire frequency in Ngarkat Reserve (**Figure 6**). Nevertheless, patches within large reserves can remain unburnt for many decades (>100 years, Clarke et al., 2010). Fire mapping for 1972–2007 (Avitabile et al., 2013) showed that despite the regular occurrence of large fires, less than 3% of mallee vegetation experienced more than one fire during this 35-year period. Pausas and Bradstock (2007) estimated the fire cycle for conservation reserves in the region (number of years to burn an area equal to the reserve) to be between 125 and 206 years.

Most wildfires burn with high severity (**Figures 7A,B**) (Clarke et al., 2010). Mallee eucalypts are short, thin-barked and many have strips of decorticating bark that bridge the vertical gap between ground fuels and canopy. Flame heights of ground-level fires readily scorch or consume the eucalypt canopy (Bradstock and Gill, 1993) and 'topkill' stems (**Figure 7B**). Thus, wildfire usually triggers a replacement of standing eucalypt stems, unlike many taller, mesic eucalypt forests and woodlands where patches of undamaged canopy within fire scars are common (Leonard et al., 2014). The homogeneous severity of wildfire is highest in areas with few topographic or moisture gradients to inhibit fire spread (such as sandplains of Triodia Mallee), although

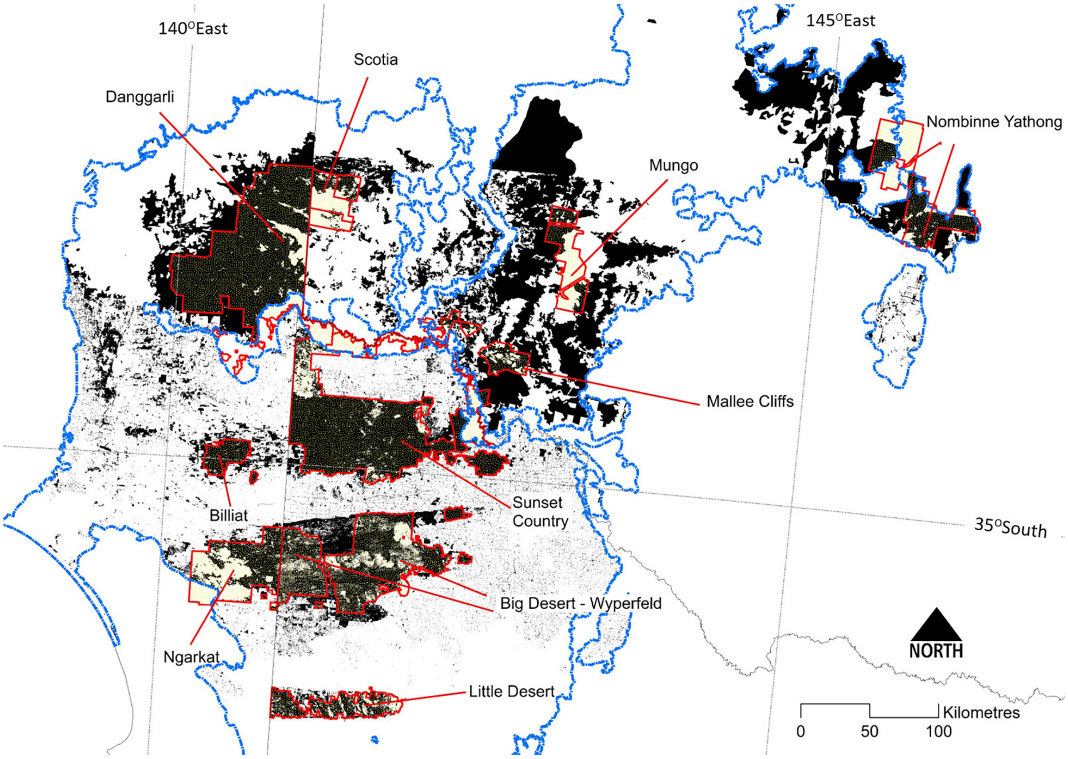

FIGURE 4 | The distribution of extant (dark shading) mallee vegetation in the Murray-Darling Depression Bioregion (Murray Mallee region) (outlined in blue). Major protected areas (including conservation reserves) are bounded in red and shaded pale yellow.

some unburnt patches do occur (Berry et al., 2015). Wildfire in contemporary mallee ecosystems typically produces a coarse-grained mosaic of large blocks of vegetation of a common seral stage (10,000s of ha in area), adjacent to other large blocks of vegetation of different seral stages (**Figures 5**, **7A**).

In addition to wildfires, land managers conduct planned burns during late autumn and early spring when climatic conditions enhance the controlled use of fire (e.g., Sandell et al., 2006; **Figure 7C**). These burns aim to impede the spread of future wildfires under more-severe conditions. They may include: (a) small scale ignition of individual *Triodia* hummocks, applied on foot, in a 50–100 m strip beside a track to remove ground-level fuels without consuming the canopy of mallee eucalypts; (b) air- or ground-ignited strategic strips several kilometers wide and tens of kilometers long that are lit from existing fire scars to reduce both ground layer and canopy fuels; and (c) patchy burning of blocks of mallee vegetation (100s ha in area) with the aim of removing ground and canopy fuels in parts of the landscape. In some cases (e.g., in Heathy Mallee), planned burns may also have an additional ecological goal, such as to trigger regeneration of serotinous plants.

Drivers of Fire Regimes

The extent and configuration of wildfires in mallee vegetation depend on multiple factors: fire-weather conditions, fuel load, and the spatial arrangement and contiguity of fuels (Bradstock and Cohn, 2002). While interactions between these variables create some heterogeneity in fire severity, extensive burnt areas are common (Avitabile et al., 2013).

'Fire weather' conditions – the combination of climatic trends and daily weather that increases the likelihood of large fires – include lightning-inducing weather changes, high temperature, low humidity, and strong gusty wind changes (Luke and McArthur, 1978; Long, 2006). Days of extreme fire weather result in vegetation dry enough to act as a continuous combustible fuel layer, prone to ignition by lightning strikes (Cheal et al., 1979; Bradstock and Cohn, 2002). In the Murray Mallee region, days of extreme fire weather occur in late spring through summer (November to March), and most fire events coincide with dry winds from the north to northwest, followed by south-westerly changes (Long, 2006).

Irregular pulses of above-average rainfall (e.g., once or twice a decade) are a driver of short-term availability of fuels due to widespread, increased cover of ephemeral grasses (**Figure 8B**) (Ludwig et al., 1990; Gibson et al., 2014, 2015). When dry, such grasses increase both the quantity and, particularly, the contiguity of fuels. In the absence of an ignition source these fine fuels are consumed by herbivores or detritivores. However, some of the largest fires in the region (e.g., 658,000 ha across New South Wales and South Australia in 1976) have occurred in summer months following a period of high rainfall (Noble et al., 1980; Avitabile et al., 2013). Similar patterns of large fires following wetter than average conditions in the preceding year have also been reported in southwestern Australia (O'Donnell et al., 2011a).

TABLE 1 | Key features of wildfire in contemporary mallee ecosystems, the factors that contribute to those features and the biotic consequences.

Features of wildfires in mallee ecosystems	Factors contributing to fire features	Biotic consequences
a. Wildfires are **large** (>10,000, with well documented fires >100,000 ha)	• When fuels are well-connected there are f**ew topographical or moisture gradient barriers** and large areas can be burnt in short periods of extreme fire weather	• Large extent of burnt patches may isolate plant and animal populations, inhibit recolonization and cause extirpation
b. Wildfires can **occur in high or low rainfall years** in late spring or summer, ignited by lightning	• Unlike much of the arid zone, annual rainfall patterns are adequate to sustain cover of perennial plants. Hot weather in late spring or summer results in vegetation dry enough to carry fire and the **risk of ignition by lightning strikes is high most years.**	• Burning of mid and late successional vegetation is a possibility most years, once fuel connectivity is re-established, a risk for many species that prefer these habitats.
c. Areas that are uniformly burnt (with no unburnt patches) are common after wildfires	• Annual rainfall patterns are sufficient to sustain cover of **perennial plants that contribute to year-round and across-year connectivity of fuels**	• For some animals and plants, recolonization of a burnt site depends on the size and proximity of source populations of colonists residing in adjacent unburnt landscapes; or in unburnt islands within the fire scar, as might occur in rocky or topographically more diverse landscapes
d. Most wildfires consume or scorch canopy foliage and topkill eucalypt stems	• Mallee eucalypts are typically smooth-barked and short; within flame height of most fires. • Canopy foliage and stems are typically killed or consumed by the fire's passage, unlike taller forests or woodlands where patches of undamaged canopy are common.	• Most above-ground plant material is consumed or killed by fire • Triggers **synchronous, uniform, slow** and **predictable recovery** of perennial plants (over a century in development) from underground meristems, canopy seedbanks or soil seedbanks, over large areas within the fire perimeter. • **Many animal species have evolved preferences for particular seral stages** in this long recovery process (as evident from five distinct recovery patterns). • Most **fire-sensitive animal species** prefer **mid to older seral stages** • **Time since fire** is a key predictor of community composition
e. Interval between fires: vegetation is **capable of carrying a fire 10–20 years** after the previous fire; sometimes even sooner (within 2 years) after a high rainfall event, but **patches within large reserves can remain unburnt for many decades (>100 years)**	• Foundational, perennial ground-layer plants (e.g., *Triodia*) take between 10 and 20 years to recover and contribute to fuel contiguity at ground level. • High rainfall events can trigger mass germination of ephemeral grasses (e.g., *Austrostipa*) that provide a short-lived continuous fuel layer at ground level.	• Some crucial habitat features can recover before the landscape can carry another fire (e.g., *Triodia* hummocks), others cannot (e.g., hollows in mallee eucalypts may not develop until 50–60 years post fire). • Most **animal species listed as threatened** have a preference for **mid to older seral stages**
f. **Clearing of mallee vegetation for agriculture has altered fire behavior** at landscape and regional scales	• Unlike the arid zone, rainfall in mallee ecosystems is sufficiently reliable to sustain cereal cropping, not just pastoralism. Consequently, vast areas of mallee vegetation on more-fertile soils have been cleared for cropping.	• Isolation of burnt patches from sources of colonists in unburnt landscapes can inhibit recolonization and cause local extinctions • Discontinuity of fuels across the landscape, and fire suppression activities, can result in remnant patches of mallee vegetation remaining unburnt for very long periods (>100 years) As a consequence of habitat loss and fragmentation, wildfires can now burn entire conservation reserves (>10,000 ha) in a single event, homogenizing the landscape to a single post-fire age class.

Bolded terms are used to highlight key points.

Stands of some plant species (e.g., *Callitris, Allocasuarina, Triodia*) can influence the passage of fire and hence the fine-scale patchiness and occurrence of unburnt patches. For example, dense stands of *Callitris verrucosa* that establish in Heathy Mallee vegetation after decades without fire (White, 2006) appear to impede the spread of fire due to transformation of the litter layer (Bradstock, 1989b) and possibly by reducing wind strength (Cruz et al., 2013). Such stands have the potential to create unburnt fire shadows in their lee (Benshemesh, 1990). In contrast, *Triodia* hummocks enhance the passage of fire by connecting fuels across the landscape (Dodson, 1982).

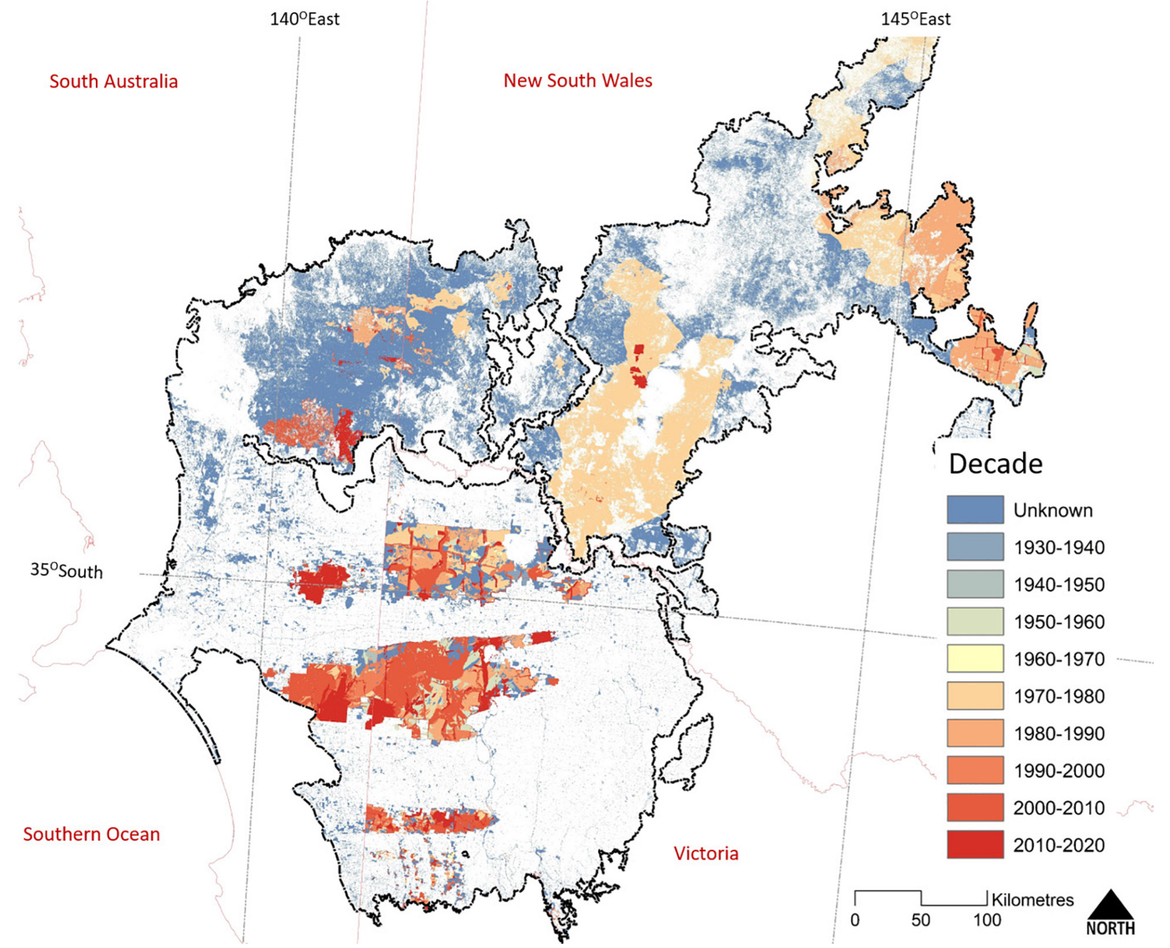

FIGURE 5 | The extent of the last known fire within extant woody vegetation across the Murray-Darling Depression Bioregion (outlined in black). State boundaries are shown in pale red. The earliest recorded fires date from the 1930s; however, reliable and systematic recording of fire extent dates back to the mid-1970s only and correlates with the regular acquisition of cloud-free Landsat imagery. Map compiled from State fire-history datasets: Victoria (Department of Environment Land Water and Planning, 2020), New South Wales (National Parks and Wildlife Service, 2020), and South Australia (Department for Environment and Water, 2016).

HOW DO FIRE REGIMES SHAPE BIODIVERSITY?

Fire regimes shape biodiversity in mallee ecosystems at multiple scales: at the local scale (e.g., 10s of ha) by triggering post-fire secondary succession, and at landscape (1000s–10,000s ha) and regional scales (100,000s ha) through the effects of spatiotemporal variation on the distribution of species. We first summarize knowledge of the response of plant and animal species at the local scale to two key aspects of the fire regime, time since last fire and fire interval, and then consider how spatial patterns of fire at the landscape and regional scale can influence the biota.

Responses to Time Since Fire and Inter-fire Interval

Vegetation

Plant species of mallee vegetation possess life-history traits that enable persistence through recurrent disturbances. Among woody species, obligate seeders predominate (Clarke et al., 2015) and the majority have soil-stored seed banks (e.g., *Acacia*, *Senna*, *Beyeria*). Serotiny (canopy seed storage) is relatively uncommon in the Murray Mallee region (e.g., *Callitris* and *Hakea* spp., Bradstock and Cohn, 2002). Traits vary along the rainfall gradient: with decreasing rainfall the proportion of obligate seeders increases while resprouting species decrease (Pausas and Bradstock, 2007).

Fire drives the structure of mallee vegetation (e.g., Gosper et al., 2012b). Wildfires topkill or consume above-ground vegetation, thus vegetation structure changes in a synchronous and relatively predictable way with time since fire as recovery occurs. Such a synchronized structural response to time since fire is more prevalent in mallee vegetation than in temperate forests where, for many tree species, epicormic re-sprouting along trunks and limbs ensures rapid recovery of the canopy after fire (Rainsford et al., 2020). Key structural components strongly influenced by time since fire include mallee eucalypts, understorey vegetation (e.g., chenopods and perennial

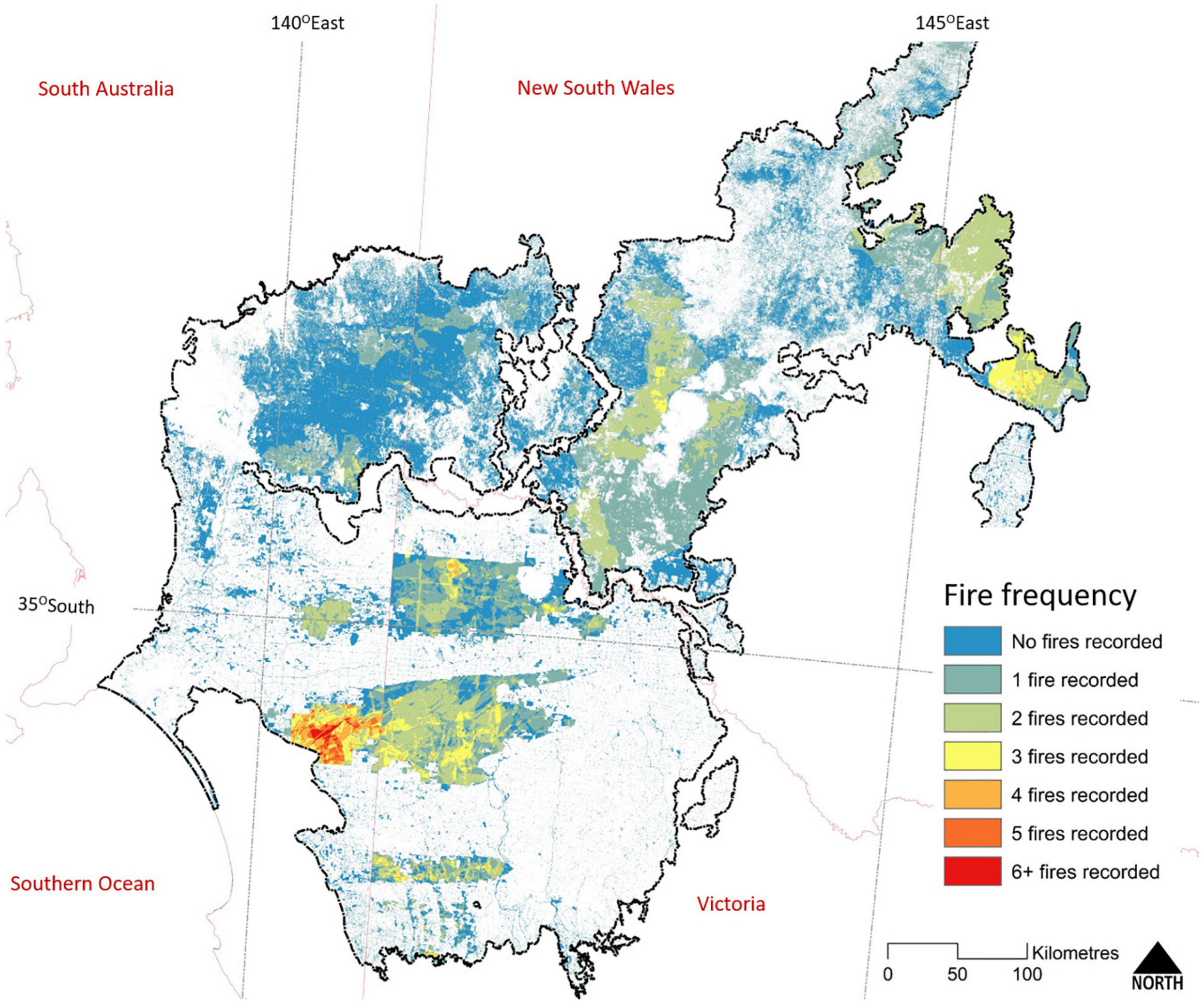

FIGURE 6 | The frequency of known fires within extant woody vegetation across the Murray-Darling Depression Bioregion (outlined in black). State boundaries are shown in pale red. The earliest recorded fires date from the 1930s; however, reliable and systematic recording of fire extent only date back to the mid-1970s and correlates with the regular acquisition of cloud-free Landsat imagery. Map compiled from State fire history datasets as for **Figure 5**.

grasses like *Triodia scariosa*), extent and cover of litter, and structural features such as tree hollows (Haslem et al., 2012; Kenny et al., 2018).

Recruitment of mallee eucalypt seedlings following fire is rare, unlike many other *Eucalyptus* species, despite the seeds being protected from fire in woody capsules: harvesting of seeds by ants may be a factor (Wellington and Noble, 1985). It is not clear what combination of triggers is needed for successful establishment of seedlings, but fire alone is insufficient. Competition with resprouting adults may also inhibit establishment of seedlings (White et al., 2003). Post-fire recruitment of eucalypt seedlings may be greater when above-average rainfall follows a fire (Wellington and Noble, 1985) and grazing pressure is low (Westbrooke and Florentine, 2005). Established mallee eucalypts typically recover from fire by sprouting dozens of stems from below-ground lignotubers (Noble, 2001). The number of stems per lignotuber declines with time since fire, accompanied by a steady increase in the height of canopy foliage (Haslem et al., 2011; Kenny et al., 2018). A decline in the density of trees with time since fire (e.g., Chenopod Mallee), and associated increases in spacing, result in reduced contiguity of fuels. In the absence of fire, or where isolated individual trees escape damage from fire, stems reach much greater sizes.

Time to senescence of mallee eucalypts is not known. Above-ground stems over 200 years in age can appear healthy and underground lignotubers may be many centuries old (Tyson et al., 1998). A difficulty in determining longevity is that there are few stands of known post-fire age greater than 100 years. Fire mapping based on satellite imagery is available only from 1972 (Avitabile et al., 2013), and the precision of other methods (e.g., modeled relationships between stem diameter and age) diminishes greatly beyond 90 years post-fire (Clarke et al., 2010;

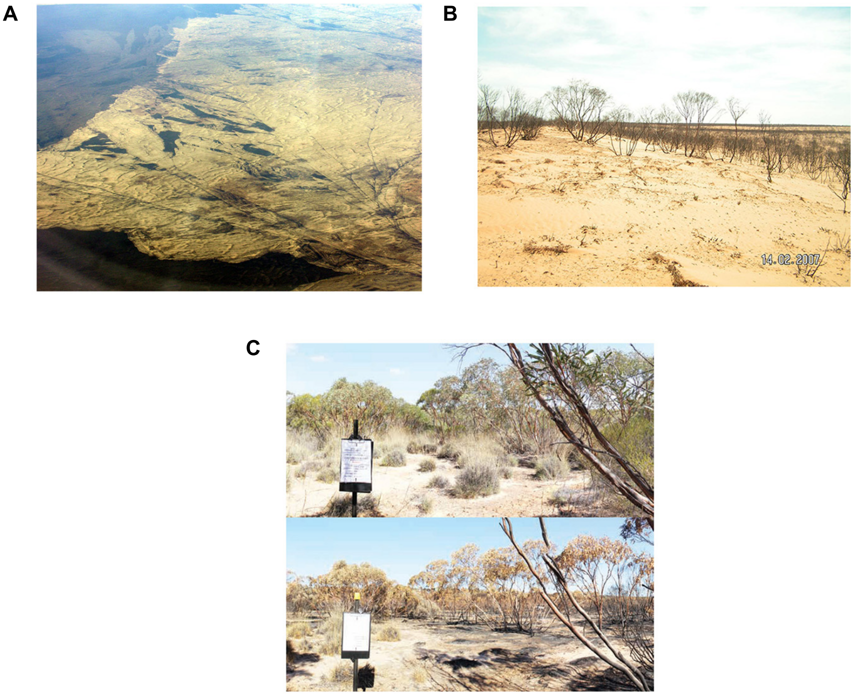

FIGURE 7 | (A) Aerial view of a large wildfire scar in the Big Desert, Victoria. **(B)** Ground-level view of Triodia Mallee recently burnt by wildfire. **(C)** Photopoint images of a site in mallee vegetation before and after a planned fire, conducted for experimental purposes.

Callister et al., 2016). The nature of successional change in mallee vegetation after prolonged absence of fire (e.g., hundreds of years) is not clear. Heathy Mallee can become dominated by *Callitris verrucosa* as other shrubs (e.g., *Banksia* spp.*)* senesce (Cheal, 2010).

Recruitment of seedlings of grass, herb and shrub species occurs within the first 2 years after fire (Noble et al., 1980; Wilson et al., 1988). In Triodia Mallee, this response is generally transitory and *Triodia* becomes the dominant species after ~5 years (Noble et al., 1980; Pickett et al., 1987; Letnic et al., 2004). This pattern differs in central NSW and the Eyre Peninsula, where *Triodia* increases after fire but shrubs remain dominant throughout (Gibson et al., 2014, 2015). The cover of *Triodia* hummocks increases steeply from ~ 5 to 20 years post-fire (Haslem et al., 2011; Kenny et al., 2018), with maximum cover at ~30 years since fire. With increasing age, cover may decline or reach a plateau, depending on soil type and topographic position (Verdon et al., 2020). The growth form of this dominant species also changes through time: with increasing post-fire age (~30 years), hummocks may die in the center but continue peripheral growth, thus forming a 'ring' of live plant material with dead material in the center. The proportion of plants occurring in 'ring form' reaches a peak at ~50 years, though hummock-form plants occur throughout the chronosequence (Kenny et al., 2018).

Stems of mallee eucalypts typically are killed by wildfire. Stem mortality is also common after high-intensity planned burns, but not all are fully consumed; some dead stems remain standing. Over time, dead stems fall and become logs, peaking in density 10–20 years after fire (Haslem et al., 2011). If the interval between the two most recent fires is long (e.g., >80 years), the diameter of these stems will be large when killed by fire. Such large dead stems can remain standing for decades and provide valuable nesting and roosting hollows for fauna (**Figure 9**). The availability of hollows provided by dead stems increases with the interval between fires (Haslem et al., 2012). Living stems typically do not develop hollows suitable for fauna until >60 years post-fire (Haslem et al., 2012). Similarly, slow development of key structural attributes has been reported in southwest Australian mallee (Gosper et al., 2012b). Although small hollows become larger over time, many are lost as stem densities decline with time since fire. Consequently, for species using medium (4.0–9.9 cm entrance diameter) and large hollows (≥10 cm), such as parrots, owlet nightjar (*Aegotheles cristatus*), larger reptiles and bats, there is a very long period before this resource becomes available, coupled with extensive areas of younger fire age-classes where hollows are effectively absent (particularly in Triodia Mallee).

The interval between fires may also affect the persistence of plant species. For example, simulated fire intervals that were too short (<20 years) or long (>50 years), both resulted in reduced population size of the obligate seeder *Callitris verrucosa* due to the elimination of juveniles and senescence of adults, respectively (Bradstock et al., 2006). In southwest Australia, mallee communities dominated by obligate seeders are less resilient to variation between inter-fire intervals than communities dominated by resprouters (Keeley, 1986; Gosper et al., 2012a,b). Considerable variability

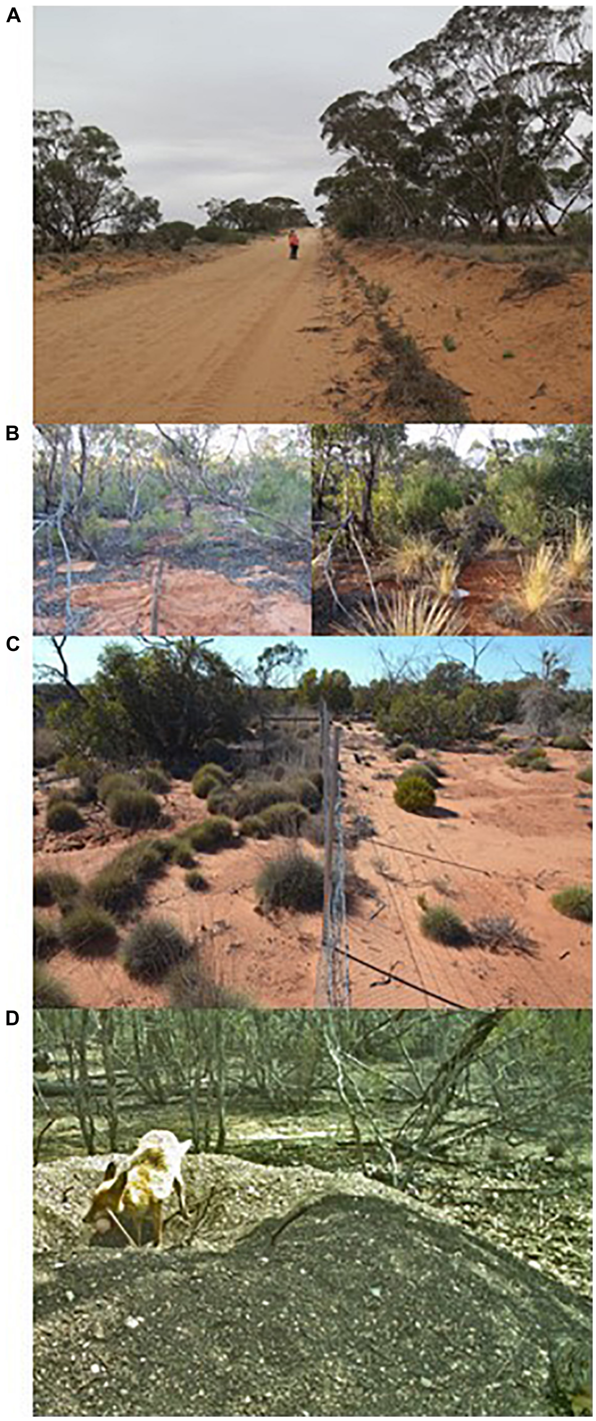

FIGURE 8 | Illustrations of drivers that interact with fire in mallee ecosystems. **(A)** Fragmentation of mallee vegetation for cereal cropping, resulting in long unburnt linear corridors. **(B)** Contrasting levels of *Austrostipa* and shrub cover in drought (2007, left) and after high rainfall (2010–2011, right) in Tarawi Nature Reserve. **(C)** Fence line comparison in Tarawi Nature Reserve showing vegetation differences in 2013 due to greater herbivory by mammals on right hand side of fence, 7 years after both sides of the fence had been burnt (photo courtesy David Keith). **(D)** Exotic predator (red fox) preying upon the egg of an ecosystem engineer (malleefowl – partially visible in lower left of frame). Photo courtesy of Riverina Local Land Services.

in the rate at which seed banks accumulate (both above and below ground) has been reported among geographically dispersed populations of obligate seeders, making determination of minimum and maximum tolerable fire intervals challenging (Gosper et al., 2013). Inter-fire interval can also influence the above-ground occurrence of plant species (Avitabile, 2014). The probability of occurrence for 14 of 43 modeled plant species was significantly affected by inter-fire interval. Nine species showed increased probability of occurrence when time between successive fires was long, with some species (e.g., *Maireana pentatropis*, *Roepera apiculata*, and *R. aurantiaca*) becoming more prevalent when the interval between fires is greater than 60–80 years (and still increasing after 90 years). Conversely, the probability of occurrence declined for three species (*Acacia sclerophylla*, *Daviesia benthamii*, and *Sclerolaena diacantha*) when the inter-fire interval was greater than 40–60 years.

Animals

With changes in vegetation composition and structure over time (**Figure 10**), the suitability of mallee vegetation as habitat for many animal species also changes (Friend, 1993; Kelly et al., 2010, 2011; Nimmo et al., 2012; Watson et al., 2012b; Smith et al., 2013, 2016). Time since fire is an important predictor of the occurrence of numerous species. Here, we identify six generalized responses to time since fire (**Figure 11**), based on occurrence of vertebrate species across a chronosequence of 100 years.

(a) *Irruptive*: Species that occur with greatest frequency of occurrence in early post-fire vegetation (<10 years since fire) tend to be those that burrow, or favor open spaces or bare ground for foraging, as the extent of such areas is high immediately after fire. Examples include the painted dragon (*Ctenophorus pictus*) and the insectivorous bird, chestnut-rumped thornbill (*Acanthiza uropygialis*). These species decline rapidly in occurrence in mid and older seral stages.

(b) *Decline*: These species, such as the desert skink (*Liopholis inornata*) and coral snake (*Brachyurophis australis*), also decline in occurrence with increasing time since fire, but in a more gradual manner (**Figure 11**). This response reflects the habitat becoming increasingly less suitable as post-fire succession proceeds.

(c) *Bell*: Species with this response type typically are associated with habitat attributes that reach their peak in mid-successional stages post-fire. For example, the southern legless lizard (*Delma australis*), the mallee ningaui and the striated grasswren are each closely associated with *Triodia* hummocks as habitat for shelter, refuge, and foraging. Their probability of occurrence peaks in mid-aged vegetation (∼20–40 years since fire) and is lower in younger and older vegetation, coinciding with reduced cover and complexity of *Triodia*.

(d) *Incline*: Species that display an incline response, such as the spiny-cheeked honeyeater (*Acanthagenys rufogularis*), striped honeyeater (*Plectorhyncha lanceolata*), Gilbert's whistler (*Pachycephala inornata*) and southern scrub-robin (*Drymodes brunneopygia*), respond to post-fire habitats that continue to

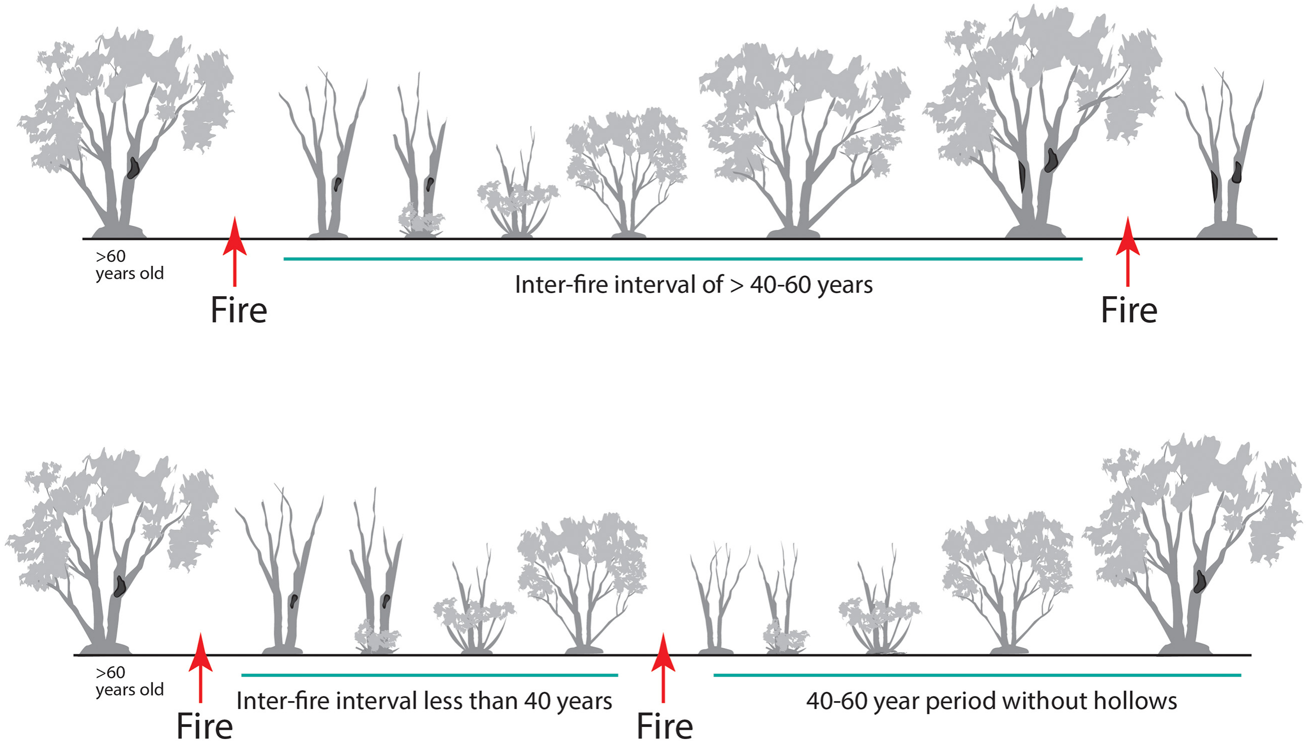

FIGURE 9 | A graphical model of changes in availability of large dead trees and tree hollow occurrence (dark patches on stems) with variation in inter-fire interval. Intervals that are too brief (<40 years) result in fewer hollows developing in live stems prior to the next fire, and fewer (dead) stems containing hollows persisting after the next fire.

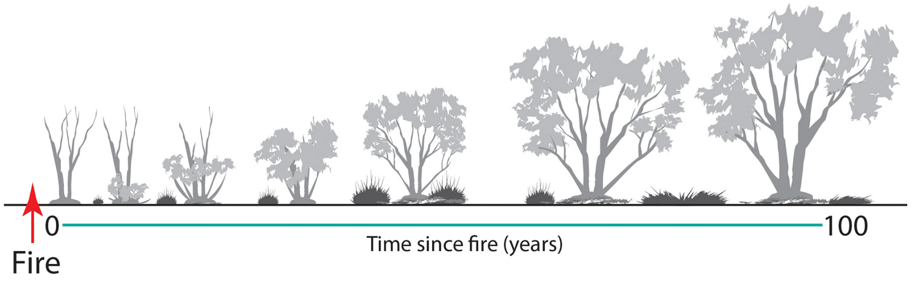

FIGURE 10 | A graphical model of structural changes in Triodia Mallee over time since fire. Highlighted is the post-fire development of mallee stems from an underground lignotuber, and changes in *Triodia* cover, litter cover and canopy height.

increase in complexity with time. The occurrence of such species showed no evidence of reaching a plateau – at least over the century time-scale studied.

(e) *Plateau*: Species that show a plateau response to fire (e.g., Murray striped skink *Ctenotus brachyonyx*, yellow-plumed honeyeater, Gould's wattled bat *Chalinolobus gouldii*) have a low probability of occurrence in early post-fire succession, reach an asymptote in mid-age vegetation and then remain at similar abundance in older vegetation. For the yellow-plumed honeyeater, for example, this pattern corresponds with the growth form of mallee eucalypts and abundance of attributes such as canopy cover, stem size and bark cover (Haslem et al., 2011), which provide foraging substrates.

(f) *Null*: In all groups studied, a substantial number of species show no significant change in probability of occurrence with time since fire; for example, 14 of 30 species of birds (Watson et al., 2012b) and 6 of 17 species of reptiles (Nimmo et al., 2012) modeled for the Murray Mallee region.

The response of species to time since fire may also vary between vegetation types and spatially between geographic areas (Nimmo et al., 2014). For example, of 17 species of reptile in the Murray Mallee region with sufficient data to model, 11 species displayed significant relationships with time since fire: nine species in Triodia Mallee, four species in Chenopod Mallee and only two in both (Nimmo et al., 2012). Similar observations were evident for bird species (Watson et al., 2012b). These results

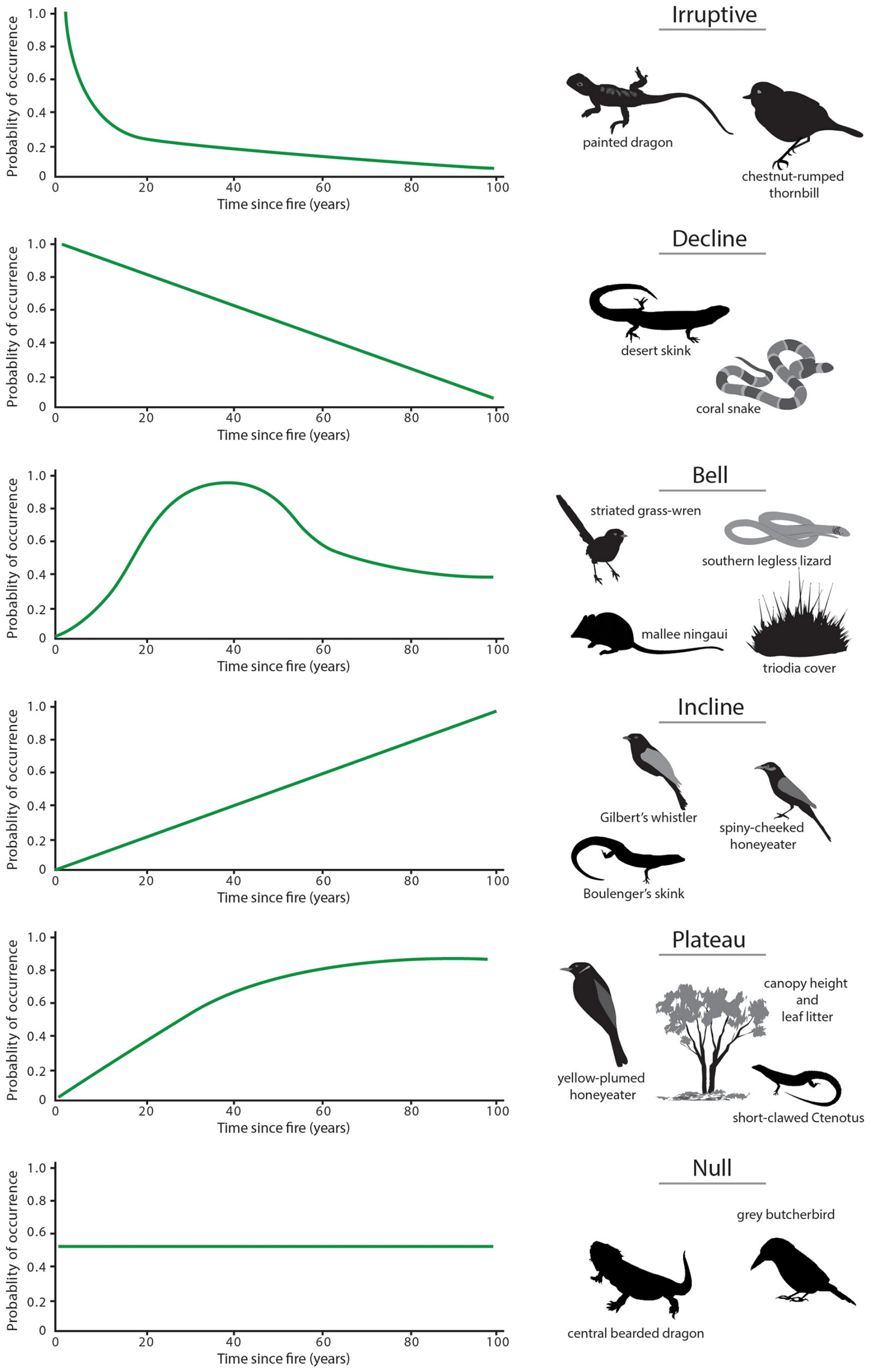

FIGURE 11 | Idealized responses of mallee fauna to time since the last fire. 'Response curves' represent six discrete patterns of the change in the probability of occurrence of a species with time since the last fire over a 100-year post-fire chronosequence: 'irruptive,' 'decline,' 'bell-shaped,' 'plateau,' 'incline,' and 'null' (or no clear response). Images are of exemplar species that showed these responses.

can be attributed to differences in vegetation composition and habitat attributes between vegetation types, and to differences in flammability.

There is a risk that the capacity to detect some species varies with time since fire and may influence apparent abundance and therefore fire response patterns (Driscoll et al., 2012, 2020). For example, some cryptic reptiles become more active after fire, increasing trap rates within a time frame too short to represent change in actual density. Such species can exhibit an apparent irruptive response, but this may be due to greater detectability, presumably related to reduced shelter opportunities and changes in prey availability (Driscoll et al., 2012). In contrast, some species may have behavioral and physiological adaptations, such as torpor, that allow them to avoid starvation or predation following fire by sheltering in place (Geiser et al., 2017; Nimmo et al., 2019). This could lead to lower detectability immediately following fire and being recorded as absent at sites where they remain but are inactive. Consequently, some uncertainty around the shape of species' responses to time since fire is difficult to resolve.

Less is known on how invertebrates respond to time since fire. In the Murray Mallee, an examination of 21 species of invertebrates from key groups (psyllids, termites, scorpions, centipedes) in Triodia and Chenopod Mallee did not detect any species exhibiting a significant response across a 100-year chronosequence (Avitabile, 2010). Many termite species nest in subterranean burrows and appear resilient to fire (Avitabile et al., 2015; Davis et al., 2018). In mallee vegetation of the Eyre Peninsula, South Australia, Teasedale et al. (2013) found no difference in abundance between post-fire age classes for 15 orders of invertebrates; but, at a finer resolution, 17 morphospecies did show such variation. Two closely related Lycosid spiders showed contrasting responses: one taxon was most abundant in early succession (4–5 years) and the other in later succession (>40 years), indicating the importance of a (morpho)species-level approach rather than broad categories (Teasedale et al., 2013). Similarly, in mallee-heath shrublands of southwestern Australia, Friend and Williams (1996) found that variation in the abundance of most Orders of invertebrates was not strongly related to fire. However, Coleoptera and Diptera were most abundant >40 years post-fire and Hemiptera and Orthoptera peaked in earlier seral stages.

While recent studies have advanced knowledge of how animal species respond to time since fire, little is known of the effects of repeated fires on their distribution and abundance in mallee ecosystems. It is likely that interactions between fire interval (or fire frequency) and vegetation structure influence habitat suitability, with mammals being the most well-studied group to date (Senior et al., 2021). For example, fires at shorter intervals (<40 years) that reduce the abundance of dead stems with hollows, reduce the suitability of habitat for species that depend on tree cavities, such as the south-eastern long-eared bat (*Nyctophilus corbeni*) (Lumsden et al., 2008; Senior et al., 2021).

Key challenges for future studies are to better understand: (a) how extreme intervals (too long or too short) influence the persistence of plants (see Gosper et al., 2013); (b) how repeated fires (and fire interval) influence animal populations; (c) how the seasonal timing of fires and (d) post-fire seasonal and annual rainfall patterns affect plants and animals.

Responses to Spatial Patterns of Fire

Fire creates a spatial pattern of burned areas and unburnt patches of different sizes and shapes (**Figure 7A**). The characteristics of fire (**Table 1**), the vertical connectivity of fuels and the limited topographic relief in mallee ecosystems mean that vegetation typically burns completely or else remains unburnt (O'Donnell et al., 2011a), rather than generating a fine mosaic of differing levels of fire severity at a local scale as commonly occurs in forest ecosystems with greater rugosity (e.g., moisture and flammability differences between ridges, slopes and gullies). Over time, additional fires occur across the landscape, thus creating a coarse-grained 'visible mosaic' comprising large (100s and 1000s ha) stands or patches of different age since the last fire (e.g., **Figure 7A**). Additional spatial complexity is created by the interval between fires: for example, two stands of mallee vegetation, both 5 years since fire, may differ in subtle ways if the interval since the previous fire was 10 years for one and 80 years for the other. The term 'invisible mosaic' refers to these spatial differences that reflect the temporal history in the landscape, but which are not necessarily visually apparent (Bradstock et al., 2005).

Spatial patterns of fire affect the biota of mallee ecosystems in several ways. The size, shape and patchiness of a fire affect the context of sites, both those burnt and those that remain unburnt. While individuals of some species (e.g., fossorial reptiles) can persist on a burnt site, a key issue for many plants and animals is the capacity to recolonise post-fire, either from internal sources within the fire boundary or external sources (Bradstock et al., 2005; Nimmo et al., 2019; Senior et al., 2021). For example, Watson et al. (2012a) found sites distant from unburnt vegetation supported fewer bird species, but those that contained small unburnt patches supported more species than uniformly burnt sites. Unburnt patches within the fire boundary (**Figure 7A**) may act as refuges where organisms can escape the fire or may assist animals to recolonise post-fire. Berry et al. (2015) found the number of bird species increased with the size of unburnt patches (1–12 ha in size) remaining in a burnt mallee landscape, but these patches had fewer bird species than large unburnt tracts outside the fire boundary. Together, these results suggest that large fires of uniform severity that homogenize landscapes to a single fire age-class may reduce faunal diversity, even of mobile taxa like birds.

Based on the observation that different species favor different stages in post-fire succession, it has been hypothesized that landscapes that have a greater diversity of post-fire age classes ('pyrodiversity') should also have a greater biodiversity (Bradstock et al., 2005; Parr and Andersen, 2006). In one of the first empirical examinations of spatial and temporal variation in pyrodiversity, faunal communities in the Murray Mallee were surveyed in a series of 28 'landscapes' (each 12.5 km^2 in area) that differed in the diversity of post-fire age-classes and extent of long-unburnt vegetation. Contrary to expectations, a positive association between species richness and the diversity of post-fire age classes was not detected at this scale, for either birds, mammals or reptiles (Kelly et al., 2012; Taylor et al., 2012; Farnsworth et al., 2014). Key influences on biodiversity included the proportion of older vegetation (>35 years-since-fire) in the landscape (birds, and the mallee ningaui) (Kelly et al., 2012; Taylor et al., 2012), environmental gradients and biogeographic barriers (reptiles) (Nimmo et al., 2013; Farnsworth et al., 2014) and recent rainfall history (rodents and pygmy-possums) (Kelly et al., 2012). Lack of a strong relationship with age-class diversity may be attributed to several factors, including that few of these faunal species occur exclusively in a particular age-class and that there are few species entirely restricted to early successional vegetation.

These findings highlight the complexity of fire management in semi-arid mallee and other ecosystems. Clearly, species show different responses to time-since-fire. Some require a minimum area of a particular post-fire age class(es) (unknown for most species) to be present to persist in the landscape. For such species, there needs to be other suitable patches developing within dispersing distance for the time in the future when the patch(es) they currently occupy are no longer suitable. Therefore, a spatial diversity of post-fire age-classes is required at larger scales (e.g., a large conservation reserve or regional network of reserves comprised of many landscape elements) to ensure a progression of seral stages will be available within dispersal distance for all species, in the long term. Modeling to identify an 'optimum' mix of fire age-classes in the Murray Mallee region indicated that a desirable mix of fire histories for biodiversity conservation includes a combination of early, mid and late post-fire age-classes, weighted toward late seral stages (Kelly et al., 2015). Detailed modeling of a wider range of seral stages clarified a preference for vegetation 11–35 and >80 years post-fire that provides critical habitat for many threatened species (Giljohann et al., 2017a). However, a key challenge for future studies is to understand how the spatial configuration of fire age-classes (patch ages, sizes, and proximity) influences species responses because, generally, little is known about dispersal. A second challenge is how such knowledge can inform management actions.

HOW DO INTERACTIONS BETWEEN FIRE AND OTHER DRIVERS SHAPE BIODIVERSITY?

Habitat Loss and Fragmentation

Fire regimes and the loss and fragmentation of habitat interact in three main ways (Driscoll et al., 2021): (a) fire can be an agent of habitat loss and fragmentation, whereby fire removes or fragments habitat, or creates and connects habitat; (b) habitat loss and fragmentation can influence fire, with a consequence being that fire regimes are altered (e.g., changes to fire ignition and spread; Parsons and Gosper, 2011); and (c) the two do not influence each other, but fire and fragmentation interact to affect the responses of the biota.

In mallee ecosystems, extensive wildfire can remove and fragment habitat for species that depend on mid to late successional vegetation or attributes associated with these stages. For example, for species strongly associated with habitat components such as *Triodia* hummocks, canopy foliage or deep litter layers, fire results in loss of habitat until it is replaced by successional regrowth (e.g., Kelly et al., 2010). Extensive fire can result in fragmentation of a species' distribution into localized populations, separated by unsuitable, early successional vegetation or farmland. This occurs, for example, for the mallee emu-wren, a small passerine dependent on mid-successional Triodia Mallee vegetation. Brown et al. (2013) found limited genetic structure within this species when it occupied continuous mallee landscapes; attributed to populations persisting via dispersal of individuals and colonization of temporally dynamic patches of suitable habitat. However, this species now has a patchy *regional* distribution across major conservation reserves (e.g., Murray-Sunset National Park) and has become locally extinct in some smaller reserves due in part to a large fire incinerating most of a reserve (i.e., Billiat Reserve) (**Figure 4**) (Brown et al., 2009; Verdon et al., 2020).

Conversely, for an early successional species, lack of fire and consequent successional change may make habitats less suitable and limit movements and population connectivity. The knob-tailed gecko (*Nephrurus stellatus*), an early successional species in mallee vegetation on the Eyre Peninsula, increases in population density for 10–15 years after fire, then declines dramatically by >30 years post-fire (Driscoll et al., 2012). Change in habitat suitability with post-fire succession results in decreased dispersal of individuals and a decrease in genetic diversity of local populations (Smith et al., 2016).

Habitat loss and fragmentation in the Murray Mallee region has also affected fire regimes. In cleared farmland landscapes, mallee vegetation typically persists as small disturbed fragments and linear networks along road reserves (**Figure 8A**). As is also the case in fragmented mallee systems in western Australia (Parsons and Gosper, 2011), small fragments now rarely experience fire due to reduced ignition, greater suppression efforts and reduced connectivity of fuels. One consequence is that with increasing post-fire age of mallee eucalypts (e.g., >80 years), stem sizes are large and tree-hollow formation has progressed to provide an important resource for hollow-dependent species (e.g., parrots, bats). Should fire occur, these isolated patches (and even larger ones like Billiat Reserve, **Figure 4**) are now unlikely to follow the same patterns of plant and animal succession as observed in larger tracts of vegetation due to isolation limiting colonization (Nimmo et al., 2019). Their post-fire faunal communities are likely to reflect the species present in surrounding modified environments (Simms et al., 2019), and result in more generalist faunal communities.

Rainfall and Drought

Rainfall interacts with fire to shape ecosystem structure and ecological processes in several ways. First, increased rainfall stimulates germination and growth of plants, whereas drought suppresses such activity. Thus, for a particular post-fire successional stage, above-average rains may result in a greater diversity of plants or disproportionate cover of species relative to a drier situation. Second, increased rainfall stimulates primary productivity, expressed in greater plant biomass and structural complexity, and increased flowering, fruiting and seeding, thus altering food resources and structural habitats for fauna. Third, changes in primary productivity and plant growth influence the likelihood of future fire, as discussed previously in Patterns and Characteristics of Fire in Mallee Ecosystems.

Repeated sampling of fauna and vegetation structure at a set of sites in the Murray Mallee region before and after a period of above-average rainfall (the Mallee Hawkeye Project; Avitabile, 2014) provided insight into the interacting effects of fire and rainfall on biota (Connell et al., 2021). Repeat surveys were conducted: (a) in 2006–2008, during the Millennium Drought; (b) in 2011–2012 during a subsequent major La Niña rainfall event; and (c) in 2014–2015, in dry conditions following the La Niña event. The Millennium Drought was one of the most severe, extended droughts on record for the Murray Darling Basin, with below-average annual rainfall from 2001 to 2009 (Leblanc et al., 2012). The following La Niña event had exceptional, drought-breaking rains which comprised the highest mean annual rainfall recorded for the Basin (Leblanc et al., 2012). The post-La Niña rainfall period had below-average rainfall. The Mallee Hawkeye Project shed new light on the impacts of drought and rainfall upon key components of the ecosystem: vegetation, birds, mammals and reptiles, outlined below.

Following above-average rainfall, there was no overall, region-wide increase in the cover of *Triodia,* unlike the post-rainfall irruption of annual grasses such as *Austrostipa* spp. (Noble and Vines, 1993). However, there was a decrease in the strength of the relationship of *Triodia* cover with time since fire. After years of average/below-average rainfall, time-since-fire had a strong effect on *T. scariosa* (Haslem et al., 2011). After 2 years of above-average rainfall, this strong effect was no longer observed (Avitabile, 2014). Further, there was biogeographic variation in the response of *Triodia* to time since fire: more arid sites showed a stronger response than sites with higher annual rainfall (Avitabile, 2014). This suggests that above-average rainfall can release time since fire related constraints on *Triodia* cover in the wetter parts of its range, but not in the more arid parts.

High rainfall had a massive effect on bird communities, more than doubling the incidence of many species and species richness at sites post-rainfall. For several years following high rainfall, there were changes to post-fire responses of some, but not all, species compared with drought conditions (Connell et al., 2021). Some, like the yellow-plumed honeyeater in Triodia Mallee, exhibited peaks of occurrence across a greater range of post-fire ages. Many other species exhibited a heightened preference for mid to older post-fire vegetation over younger age-classes following wetter conditions. Connell et al. (2021) suggested the longevity of rainfall effects on ecosystems might itself have a successional basis, whereby resources boosted by rainfall persist for longer periods in older fire-age classes than in recently burned vegetation.

Capture rates of rodents (house mouse *Mus musculus*, Bolam's mouse *Pseudomys bolami*) and the western pygmy possum (*Cercartetus concinnus*) are associated with higher antecedent rainfall (Kelly et al., 2013). Seed set by grasses following pulses of heavy rainfall provide short-term food resources that may result in population increases of granivorous small mammals and birds (Kelly et al., 2013; Connell et al., 2021).

Overall, reptile responses to time since fire did not change appreciably between low and high rainfall periods. For example, capture rates of the southern legless lizard were highest in mid-successional vegetation (bell-shaped response) during both survey periods; and for the mallee dragon (*Ctenophorus fordi*) in early successional vegetation, irrespective of high or low rainfall period (Avitabile, 2014).

The multi-taxa, long-term data set amassed during the Mallee Hawkeye Project highlights how important the climatic context is on the effects of fire on biota. It suggests species may be more vulnerable to wildfire or planned fire under certain climatic conditions than others—for example, planned fires conducted in preferred post-fire age classes (e.g., older vegetation) during periods when a species' population is low (e.g., following prolonged drought) may pose high risk (Clarke, 2008). Further monitoring is needed to understand the longevity of the beneficial effects of high rainfall events to biota.

Herbivory

Herbivory interacts with fire to influence the distribution and abundance of biota, primarily through differential levels of herbivory in post-fire successional stages. Here, we focus on vertebrate mammalian herbivores, but note that the role of herbivory by invertebrates (e.g., termites, psyllids, ants, locusts and grasshoppers) is likely to be profound – though poorly understood and documented. Mammalian herbivores include native species (e.g., western grey kangaroo *Macropus fuliginosus*, red kangaroo *M. rufus*) and introduced exotic species (e.g., goat *Capra hircus*, European rabbit, brown hare *Lepus capensis*). Some native herbivores are now regionally extinct (e.g., stick-nest rat *Leporillus conditor*) whereas others (e.g., western grey kangaroo) are probably more abundant than historically, due to loss of top-order predators and provision of permanent water for stock.

Herbivory can threaten a range of rare plant species (Sandell, 2006; Cheal, 2009), especially palatable species, as it affects their rates of survival, growth, reproduction and recruitment. It can shift community composition toward dominance by unpalatable species (Keith and Tozer, 2012). The threat is greatest in early post-fire succession when ephemeral species establish and otherwise-unpalatable plants are at their most vulnerable (Cohn and Bradstock, 2000).

The interaction of frequent fire and herbivory results in an even greater impact than just fire alone (Driscoll et al., 2012; Keith, 2012). The effect of herbivory on vegetation recovery post-fire has broader ecological implications when it affects the structural habitat components or food sources of other animals (**Figure 8C**). For example, grazing pressure on the regeneration of a foundation species such as *Triodia* (Cohn and Bradstock, 2000) could have detrimental effects on *Triodia*-specialist vertebrates if regeneration is inhibited.

The interaction between herbivory and fire can also vary as a function of abiotic conditions (particularly rainfall). After monitoring herbivore exclusion and control plots for more than a decade following fire and a flood at Nagaella Station in NSW, Florentine et al. (2015) concluded that flooding and herbivory combined led to greater long-term modification of vegetation composition and structure than did fire alone. In an experimental study (Giljohann et al., 2017b) that spanned the 'Millennium Drought' and subsequent record-breaking rainfall, *Triodia* recruitment and post-fire regeneration were markedly reduced by mammalian herbivory when below-average rainfall followed *prescribed* fires. In contrast, mammalian herbivory following *wildfire* had a minor effect on recruitment and post-fire regeneration during the same period (Giljohann et al., 2017b). Herbivory may be more intense in smaller burnt areas where herbivores are attracted to congregate at higher densities and benefit from the juxtaposition of shelter and foraging areas in unburnt and recently burnt areas, respectively.

There is potential for the interaction between herbivory and fire to have major, long-term impacts on the structure, composition and distribution of mallee communities. However, the unpredictable and idiosyncratic nature of major rainfall events and fires, coupled with the slow recovery rates of vegetation highlight the value of the opportunistic establishment of herbivore exclusion and control plots that can be monitored over decades following such events. Only by committing to long-term monitoring will a deeper understanding of these crucial, but dynamic, interactions be gained.

Predation

The role of top-order predators, notably the dingo (*Canis dingo*) as a keystone species that influences ecosystem structure and function in arid Australia, is increasingly recognized (Letnic et al., 2009, 2012). Two main mechanisms are proposed. First, by reducing the activity and abundance of feral and native herbivores (e.g., feral goats, large macropod species), dingoes contribute to a cascade of positive effects for plant and animal species at lower trophic levels. Second, by regulating meso-predator abundance and behavior there can be benefits for populations of prey species, including threatened small mammals (Ritchie et al., 2012; Hunter et al., 2018).

In semi-arid mallee ecosystems, the mammalian predator community has changed markedly since European colonization (Bennett et al., 1989). The dingo, formerly widespread and common, is persecuted by livestock graziers via trapping and poisoning, and no longer occurs in many areas in the Murray Mallee. Dingoes persist in the Big Desert-Wyperfeld system, are occasionally seen in the Little Desert, but are rare elsewhere. Native quolls (*Dasyurus* spp.) have been eliminated. Two exotic and invasive 'meso-predators,' the red fox (**Figure 8D**) and cat, are widespread. There is some evidence that foxes avoid, or are suppressed by, dingoes in the Big Desert (Geary et al., 2018): fewer foxes were recorded in areas with more signs of dingoes. Such an outcome may benefit native prey of foxes, including threatened or near-threatened species (e.g., Mitchell's hopping mouse, malleefowl), but this requires further examination.

Fire can potentially interact with predation (Geary et al., 2020). Fire changes the structure of habitats by removing vegetative cover and refuges, making prey species more exposed to predation. A more-open structure in recently burned areas may result in both a localized increase in predator activity and greater hunting success, both of which can result in increased mortality of prey species and limit post-fire population recovery (Doherty et al., 2015; Hradsky, 2020). This is likely to occur in mallee ecosystems, but further work is required to quantify variation in predation in relation to post-fire succession.

FIRE AND INTERACTING DRIVERS IN A CHANGING CLIMATE

In an era of a changing global climate, it is essential to consider how semi-arid mallee ecosystems will respond to future perturbations. Given predicted climate changes for the region (**Table 2**), we consider two pressing questions: (a) how might fire regimes and other interacting drivers be affected by climate change? and (b) which elements of the biotic environment have the capacity to respond to changes in these drivers and which do not?

The most recent climate forecasts for the Murray Mallee region suggest the next 10 to 30 years will be characterized by higher temperatures, reduced humidity, higher evaporation rates, longer and more severe droughts, greater variability in the quantity and timing of major rainfall events, and fewer frosts (**Table 2**). The northern parts of the region are forecast to experience a climate with more similarities to the arid zone than the semi-arid (Clarke et al., 2019).

At a regional scale, these climatic changes are forecast to result in a 50% increase in the number of days of extreme fire danger, and a fire season that starts earlier and is longer in duration. Thus, potential changes to fire regimes, along with climatic changes in water availability, are likely to have extensive ecological ramifications. Other drivers (e.g., topography, soils, biogeographic history) will constrain the ability of the biota to cope with these changes.

Whether climatic changes in mallee ecosystems cause fire activity to increase or decrease will depend on the interplay between four 'switches' (sensu Bradstock, 2010), including biomass growth, availability of fuel, fire weather, and ignition sources. On the one hand, vegetation growth and fuel accumulation may decline under reduced annual rainfall – and

TABLE 2 | Climate projections for Mildura under a medium (RCP4.5) emissions reduction scenario (Clarke et al., 2019).

Climate attribute	Change by 2020–2039 (median, 10th and 90th percentile)	Change by 2040–2059 (median, 10th and 90th percentile)
Droughts		
Annual maximum daily temperature	+1.1 (0.8 to 1.4)°C	+1.7 (1.0 to 2.0)°C
Annual rainfall	−6% (−11 to +3)	−5% (−17 to +1)
Relative humidity	−1.9% (−3.2 to −0.2)	−2.6% (−4.5 to −0.3)
Pan evaporation	+14.4% (9.9 to 22.1)	+24.5% (10.3 to 29.3)
Heavy rainfall events		
Percentage change in the 1-in-20-year maximum daily rainfall compared to 1986–2005	+1% (−11 to +7)	+3% (−14 to +26)
Frosts		
	Expected to become less frequent	
Fire danger		
	Fire season to become longer and start earlier Days of extreme fire danger (when the Forest Fire Danger Index is >95th percentile for 1986–2005) per annum to increase by 9.1 days per year (i.e., a 50% increase) by the 2050s under high emissions (RCP 8.5) scenario	

considered in isolation might be expected to reduce fire activity. On the other hand, higher temperatures may promote greater availability of dry fuel and increased fire activity (O'Donnell et al., 2011a). The occurrence of dry lightning is suggested to increase in Mediterranean climates, like mallee ecosystems, under climate change (Mariani et al., 2018; Dowdy, 2020). The relationships between these switches and their outcomes require testing but we can use ecological knowledge to explore alternative scenarios of potential fire regime change.

First, an increase in fire frequency in the Murray Mallee region could have a negative impact on many species, given that resources required by some are still developing more than a century after a fire (Haslem et al., 2011) and that a significant proportion of faunal species do not reach their peak abundance until 30 or more years post-fire. Second, if fires become more extensive, severe and even less patchy, it is likely to affect less-mobile species with limited capacity to relocate to unburnt patches, or recolonize from outside the fire perimeter, especially where mallee vegetation has been fragmented by agriculture. Third, under a drier climate scenario, the rate at which vegetation recovers after fire (e.g., years to first flowering or seeding) will likely be slowed, contributing to what has been termed an 'interval squeeze' (Keeley et al., 2005; Enright et al., 2015). Thus, insufficient seeds are produced between fires to replace individuals killed by the previous fire, leading to local extinction. Alternatively, if climate change results in a scenario of reduced fire activity, this may be easier to manage; strategic use of planned fire could be used to trigger germination of plants that require more fire, or to create habitat for animals that prefer early or mid-successional habitats.

A changing climate will also affect diverse processes that interact with fire in shaping mallee ecosystems. Decreased moisture availability could profoundly affect processes by which carbohydrates become available to heterotrophs. For example, if eucalypt flowering becomes less frequent and less seasonal under a drying scenario, this could affect the survivorship and reproductive success of both resident and nomadic nectarivores (Keast, 1968). Similarly, climate-driven declines of psyllids, which produce carbohydrate-rich lerps eaten by many invertebrates and vertebrates (Paton, 1980), would likely diminish the capacity of these heterotrophs to recover after fire.

Desiccation and degradation of cryptogamic soil crusts under a drying climate will likely result in increased wind and water erosion and accompanying loss or redistribution of soil nutrients. Dust storms, previously triggered by overgrazing and clearing of native vegetation (Broome et al., 2020) may become more common with longer dry periods under climate change (Speer, 2013). The regional loss of nutrients is likely to take centuries to recover, but the potential effects on post-fire recovery of the biota are unknown.

A further issue concerns the capacity of biota to respond to extreme events, both droughts and wet years, which have long-lasting impacts. While the abundance of some bird species more than doubled after wet years, populations of some endangered birds did not recover from drought even after high rainfall (Connell et al., 2021). Species able to rapidly capitalize on unpredictable flushes of resources may benefit from an increased likelihood of major rainfall events. Whether such events will be sufficiently frequent for species to recover and avoid local extinction during longer and more severe droughts, is unclear. The subdued topography of mallee ecosystems and their nutrient-poor soils appear to offer little in the form of permanent drought refuges. Nevertheless, there remains much to learn about how variation in habitat suitability is associated with topography (Selwood et al., 2019; Verdon et al., 2019). Much will depend on a species' ability to move between resources (Nimmo et al., 2019), and whether habitat connectivity enables such movement.

WHERE TO FROM HERE?

Mallee ecosystems have extraordinary value for the conservation of biodiversity in Australia: they support a diverse and distinctive flora and fauna, including many species of threatened conservation status, some critically endangered. Although extensively cleared for agriculture, large areas remain in conservation reserves allowing opportunities for pro-active conservation and management.

Conservation Priorities in a Flammable Ecosystem

Primary challenges for conservation in mallee ecosystems in relation to fire are: (a) to determine what 'desirable' fire mosaics, with sufficient older seral stages to sustain the biota in the long-term, look like at local and regional scales and (b) how best to achieve these through a combination of planned fire, wildfire prevention and suppression, and other active management.

A key goal in fire management is to protect and foster the development of older post-fire age classes in all regional blocks of mallee vegetation, while avoiding a single wildfire burning an entire reserve. The predicted worsening of fire weather and climatic conditions (**Table 2**) suggest that natural ignitions and uncontrolled wildfire will deliver sufficient younger post-fire age classes to accommodate species with a preference for early successional stages. Protecting key habitats will be enhanced by a capacity to link knowledge of species distributions in relation to post-fire succession and environmental variation with 'real world,' spatially explicit simulations of alternative fire management strategies. This will assist fire managers to evaluate the risks and benefits of different combinations of fire management actions. Monitoring of fuels and vegetation recovery, and a willingness to adjust burning prescriptions in an adaptive manner, will be crucial.

Management interventions that reduce the detrimental impacts of drivers that interact with fire will assist plant and animal populations to thrive post-fire and recover in good climatic seasons after disturbance. These include sustained efforts to reduce or eliminate feral herbivores and predators, and the resources on which they rely (e.g., artificial watering points; James et al., 1999). We must also anticipate climatically induced shifts in the distribution of foundation species (e.g., *Triodia*), and potential invasive species (e.g., buffel grass *Cenchrus ciliaris*) (Read et al., 2020) that would cause major changes to fire regimes. Both affect the connectivity of ground fuels (Gibson et al., 2014).

Such changes could result in irreversible losses of biodiversity on a regional scale.

Protecting and maintaining existing native vegetation is a high priority, particularly large contiguous blocks (on both public and private lands) of sufficient scale to enable internal recolonization following disturbance events, such as wildfire. Enhancing the effectiveness of crucial corridors for dispersal, including mesic woodlands along major river systems and north-south connections along climatic gradients, will support resilience to a changing climate. Likewise, increasing the contiguity between remaining areas of native vegetation, particularly conservation reserves separated by croplands, is an ambitious goal, but such broad-scale revegetation is being undertaken successfully (Koch, 2015; Berkinshaw et al., 2016) and must be commensurate to the magnitude of the challenge facing the extraordinary biota of this region.

Reintroduction of species historically present offers exciting opportunities for the conservation of threatened species and the restoration of ecosystem function (Hayward et al., 2016). Several such mammal species (e.g., brush-tailed bettong *Bettongia penicillata*, burrowing bettong *B. lesueur*, greater bilby *Macrotis lagotis*) function as ecosystem engineers and as such may play a

TABLE 3 | Knowledge gaps and research priorities relating to how fundamental components of mallee ecosystems operate.

Knowledge gaps relating to fire regimes	Why this question needs to be addressed
How do fire regimes shape biodiversity?	
1. What role does fire play in triggering seedling recruitment in foundation species (e.g., mallee eucalypts, *Triodia*)?	Knowledge of how to recruit foundation species in degraded landscapes is essential for habitat restoration efforts.
2. What constrains seedling recruitment in foundation species?	Understanding what constrains or enhances recruitment should inform management interventions.
3. How variable are the post-fire recovery responses of a taxon across a region?	Estimates of minimum and maximum tolerable fire intervals based on vital attributes of plant species underpin the timing of ecological burning. It is crucial these estimates take into account geographical and climatic variability across the region.
4. To what degree is recolonization of regenerating habitat constrained by a species' dispersal ability?	Habitat suitability modeling routinely assumes all suitable habitat is within the dispersal distance of the focal species (i.e., accessible). Knowledge of the actual dispersal capacity of the species is crucial to refining these models.
5. What is the fate of mallee vegetation from which fire is permanently excluded?	Much of the oldest mallee vegetation in the region is located in isolated, long-unburnt fragments. It is unclear if it will undergo a state change in the absence of fire.
How do interactions between fire and other drivers shape biodiversity?	
6. What is the impact upon biodiversity of the interaction between habitat fragmentation and altered fire regimes?	Since much mallee vegetation has been fragmented, it is important to understand how fragmentation and isolation alter fire regimes and affect the biota.
7. How does rainfall (e.g., quantity and timing) influence recovery rates of flora and fauna post-fire?	Knowledge of the impact of droughts and high rainfall years is crucial to predicting the likely capacity of flora and fauna to recover after fire.
8. To what extent does herbivory influence fuel loads and the recovery rate of mallee vegetation post-fire?	Elevated abundance of native and introduced herbivores has the potential to affect the rate of fuel accumulation, the composition and structure of vegetation communities, and the rates at which they recover after fire - all potentially major influences on biodiversity.
9. To what extent do native and introduced predators influence the abundance and distribution of herbivores and ecosystem engineers?	Quantifying the impact of native and introduced predators on herbivores and ecosystem engineers (e.g., malleefowl) should inform initiatives aimed at restoring ecological processes to mallee ecosystems.
10. To what extent can ecosystem engineers influence the distribution of fuels, nutrients and attributes of the fire regime (e.g., extent, frequency, interval, severity, spatial configuration)?	The ecological consequences of the loss of fossorial mammals from mallee ecosystems is poorly understood. Reintroduction of these species has the potential to influence fire regimes, nutrient cycles and vegetation recovery.
Fire and interacting drivers in a changing climate	
How will forecast changes in climate influence:	
11. The seasonal timing, frequency, inter-fire interval, extent/area and severity of wildfires?	Forecast shifts in the frequency, timing, severity and magnitude of droughts and high rainfall events create great uncertainty about how fire regimes will change.
12. The generation rates of critical resources (e.g., nest hollows, litter layers) by decomposers and detritivores?	More prolonged droughts may reduce the activity of decomposers and detritivores, slowing the development of nest hollows, while also potentially increasing the accumulation of litter and contiguity of fuels
13. The availability of key sources of carbohydrates (e.g., nectar, honey dew and lerp)?	Access to sufficient carbohydrates underpins the reproductive cycles of many vertebrates in mallee ecosystems. More spasmodic rainfall may affect the frequency and duration of breeding events.
14. The post-fire recovery rates of plant and animal species?	More prolonged droughts could impede the recovery rates of plant and animal species after fire
15. Invasion by exotic weeds and pests?	Changing climate may facilitate the invasion of mallee ecosystems by novel weeds and pests, which could change fuel availability and therefore fire regimes.

role in moderating fire regimes. Current trials of reintroductions of these and other species in several locations (e.g., Scotia Sanctuary, Mallee Cliffs NP) could pave the way for wider efforts, although control of introduced predators is a necessary and formidable challenge.

Conservation of mallee ecosystems will also require ongoing vigilance and response to changes in human land-use. Such changes in coming decades may include changes in agricultural practices and products in response to climate change; increased human access, roading and recreational use within mallee ecosystems; the introduction and spread of new invasive weeds; increased isolation and reduced capacity for dispersal by species; and the potential for new exploitative uses of mallee vegetation to provide products for human society.

Research Priorities

Despite the extensive body of research summarized in this review, two crucial questions still need *place-based* solutions if the insights gained are to be translated into on-ground actions that will enhance the conservation of mallee biodiversity.

> *1. What fire regimes should be fostered, and at what scale, to sustain biodiversity in mallee ecosystems?*

While scientists are applauded for discovering principles or insights with global applicability, land managers are judged by whether their interventions in particular locations and times lead to desired outcomes. The latter's place-based focus has the potential to align with the deep appreciation of 'place' inherent in Indigenous peoples' understanding and application of fire. For example, insights into the use of fire in semi-arid environments (including mallee vegetation) by Indigenous Ngadju people in southern Western Australia (Prober et al., 2016) highlight a place-based approach to where, when and how fire is applied (including some locations where fire is excluded). Use of fire is tailored to actual places, takes into account the idiosyncratic effects of drought/wet cycles due to unique topography, soils, waterbodies, vegetation and rock formations; and recognizes the need to protect important resources. Effective partnerships and collaboration with Indigenous people in the management of mallee ecosystems offer new opportunities, including fostering Indigenous knowledge of fire and its cultural benefits. The challenge is how to translate general principles about the fire ecology of a region into place-based solutions that effectively conserve ecological assets and cultural values.

Addressing this over-arching question requires still further attention to outstanding ecological questions relating to how mallee ecosystems function (**Table 3**, questions 1–5). The better key ecological drivers and how they interact (**Table 3**, questions 6–15) are understood, the better equipped multiple stakeholders will be to explore likely future scenarios and the potential impacts of interventions (**Table 4**), and so make informed choices between specific place-based management actions.

> *2. When and where should conservation actions be undertaken to achieve desirable fire regimes and avoid undesirable fire regimes?*

Most insights into the role of fire in mallee ecosystems have been gained from correlational studies (e.g., sampling designs based on space-for-time substitution) or long-term monitoring of 'treatment' sites without matching controls, rather than through controlled experimental manipulations. Nevertheless, management interventions – such as wildfire suppression, planned burning, weed and pest control – are regularly applied, often in the absence of rigorous monitoring of outcomes. We propose that this second over-arching question can be addressed by spatially explicit scenario modeling, combined with experimental and opportunistic application of management interventions (**Table 4**) that are routinely monitored to determine their ecological outcomes. Adopting a genuinely experimental and adaptive approach to management interventions could produce deeper ecological insights into how mallee ecosystems function, and also more relevant, spatially explicit solutions to the challenges these systems face.

TABLE 4 | Knowledge gaps and research priorities relating to management interventions.

	Knowledge gaps relating to interventions
1. *Wildfire suppression* – Which fuel modification and wildfire suppression methods are most effective in reducing the extent and severity of wildfires, at which locations, under what weather conditions and at what cost?	Management agencies responsible for mallee ecosystems use different strategies to reduce the extent and severity of wildfires, with limited, rigorous place-based monitoring of the effectiveness or cost.
2. *Ecological burning* – Where and when will it be ecologically beneficial to add fire to a landscape?	Much remains to be learnt about the vegetation types, extents and locations in which ecological burning is necessary to achieve desirable fire regimes.
3. *Predator control* – Where, when and how often will predator control be necessary to achieve desirable fire regimes?	Feral cats and red foxes have a devastating impact on mallee fauna. Their effective control has the potential to be transformational for mallee ecosystems.
4. *Herbivore control* – Where, when and how often will herbivore control be necessary to achieve desirable fire regimes?	Feral goats, rabbits and overabundant macropods can affect the recovery of mallee vegetation after fire. It is unclear if the additional stress they impose on mallee ecosystems will be increased or reduced under climate change.
5. *Weed control* – Which weeds pose the greatest threat to achieving desirable fire regimes? Where, when and how often will weed control be necessary?	With changing climatic conditions, vigilance is needed to detect and manage novel invasive species that could drastically alter fuel contiguity and fire regimes.
6. *Restoring landscape connectivity* – Where will habitat restoration achieve the greatest reduction in risk of extinction due to adverse fire regimes?	Given the forecast changes to climate, the fragmented distribution of mallee vegetation and the limited dispersal capacity of some species, strategic targeting of sites for habitat restoration to improve connectivity will enhance ecological resilience.

AUTHOR CONTRIBUTIONS

MC and AB led the Mallee Hawkeye Project, they assembled and edited the manuscript with significant assistance from LK, KG, and AH. All authors contributed to the conceptual development of the manuscript and provided review and edits across the manuscript.

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REFERENCES

Andersen, A. N. (1982). "Seed removal by ants in the mallee of northwestern Victoria," in *Ant-Plant Interactions in Australia*, ed. R. Buckley (Netherlands: Springer), 31–43. doi: 10.1007/978-94-009-7994-9_5

Andersen, A. N. (1983). Species diversity and temporal distribution of ants in the semi-arid mallee region of north-western Victoria. *Aust. J. Ecol.* 8, 127–137. doi: 10.1111/j.1442-9993.1983.tb01600.x

Andersen, A. N., and Yen, A. L. (1985). Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Aust. J. Ecol.* 10, 25–30. doi: 10.1111/j.1442-9993.1985.tb00860.x

Archibald, S., Lehmann, C. E. R., Gómez-Dans, J. L., and Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci. U.S.A.* 110, 6442–6447. doi: 10.1073/pnas.1211466110

Avitabile, S. (2010). *The Effect of Fire Regimes on the Biodiversity of Selected Invertebrates in the Murray Mallee Habitats of South-Eastern Australia*. Ph.D. thesis. Melbourne, VIC: La Trobe University.

Avitabile, S. (2014). *Mallee Hawkeye Project: Final Report 2011-2014*. Melbourne, VIC: Department of Environment and Primary Industries.

Avitabile, S. C., Callister, K. E., Kelly, L. T., Haslem, A., Fraser, L., Nimmo, D. G., et al. (2013). Systematic fire mapping is critical for fire ecology, planning and management: a case study in the semi-arid Murray Mallee, south-eastern Australia. *Landsc. Urban Plan.* 117, 81–91. doi: 10.1016/j.landurbplan.2013.04.017

Avitabile, S. C., Nimmo, D. G., Bennett, A. F., and Clarke, M. F. (2015). Termites are resistant to the effects of fire at multiple spatial scales. *PLoS One* 10:e0140114. doi: 10.1371/journal.pone.0140114

Barengi Gadjin Land Council (2017). *Country Plan: Growing What is Good. Voices of the Wotjabaluk Nations*. Horsham VIC: Barengi Gadjin Land Council.

Bell, K. J., Doherty, T. S., and Driscoll, D. A. (2021). Predators, prey or temperature? Mechanisms driving niche use of a foundation plant species by specialist lizards. *Proc. R. Soc. B Biol. Sci.* 288:20202633. doi: 10.1098/rspb.2020.2633

Bennett, A. F., Lumsden, L. F., and Menkhorst, P. W. (1989). "Mammals of the mallee region of southeastern Australia," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Melbourne, VIC: CSIRO Publishing), 191–220.

Bennett, A. F., Lumsden, L. F., and Menkhorst, P. W. (2006). Mammals of the Mallee region, Victoria: past, present and future. *Proc. R. Soc. Vic.* 118, 259–280.

Benshemesh, J. (1990). "Management of Malleefowl with regard to fire," in *The Mallee Lands: A Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (Melbourne, VIC: CSIRO Publishing), 206–211.

Berkinshaw, T. D., Durant, M., and Koch, P. J. (2016). *WildEyre Conservation Action Planning Report June 2015. Report to the WildEyre Working Group*. Brisbane: Greening Australia.

Berry, L. E., Lindenmayer, D. B., and Driscoll, D. A. (2015). Large unburnt areas, not small unburnt patches, are needed to conserve avian diversity in fire-prone landscapes. *J. Appl. Ecol.* 52, 486–495. doi: 10.1111/1365-2664.12387

Black, A., Dolman, G., Wilson, C. A., Campbell, C. D., Pedler, L., and Joseph, L. (2020). A taxonomic revision of the Striated Grasswren *Amytornis striatus* complex (Aves: Maluridae) after analysis of phylogenetic and phenotypic data. *Emu* 120, 191–200. doi: 10.1080/01584197.2020.1776622

Bliege Bird, R., and Nimmo, D. (2018). Restore the lost ecological functions of people. *Nature Ecol. Evol.* 2, 1050–1052. doi: 10.1038/s41559-018-0576-5

Bowler, J. M., Johnston, H., Olley, J. M., Prescott, J. R., Roberts, R. G., Shawcross, W., et al. (2003). New ages for human occupation and climate change at Lake Mungo. Australia. *Nature* 421, 837–840. doi: 10.1038/nature01383

Bowler, J. M., and Magee, J. W. (1978). Geomorphology of the Mallee Region in semi arid northern Victoria and western New South Wales. *Proc. R. Soc. Vic.* 90, 5–25.

Bradstock, R. A. (1989a). "Dynamics of a perennial understorey," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Victoria, VIC: CSIRO Publishing), 141–154.

Bradstock, R. A. (1989b). "Relationship between fire regimes, plant species and fuels," in *The Mallee Lands – a Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (East Melbourne, VIC: CSIRO), 218–223.

Bradstock, R. A. (2010). A biogeographic model of fire regimes in Australia: current and future implications. *Glob. Ecol. Biogeog.* 19, 145–158. doi: 10.1111/j.1466-8238.2009.00512.x

Bradstock, R. A., Bedward, M., and Cohn, J. S. (2006). The modelled effects of differing fire management strategies on the conifer *Callitris verrucosa* within semi-arid mallee vegetation in Australia. *J. Appl. Ecol.* 43, 281–292. doi: 10.1111/j.1365-2664.2006.01142.x

Bradstock, R. A., Bedward, M., Gill, A. M., and Cohn, J. S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildl. Res.* 32, 409–423. doi: 10.1071/wr02114

Bradstock, R. A., and Cohn, J. S. (2002). "Fire regimes and biodiversity in semi-arid mallee ecosystems," in *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*, eds R. A. Bradstock, J. E. Williams, and A. M. Gill (Cambridge: Cambridge University Press), 239–258.

Bradstock, R. A., and Gill, A. M. (1993). Fire in semi-arid, mallee shrublands: size of flames from discrete fuel arrays and their role in the spread of fire. *Int. J. Wildl. Fire* 3, 3–12. doi: 10.1071/wf9930003

Broome, R., Fahey, C., Gaynor, A., and Holmes, K. (2020). *Mallee Country: Land, People, History*. Clayton: Monash University Publishing.

Brown, S., Clarke, M., and Clarke, R. (2009). Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the mallee emu-wren (*Stipiturus mallee*). *Biol. Conserv.* 142, 432–445. doi: 10.1016/j.biocon.2008.11.005

Brown, S. M., Harrisson, K. A., Clarke, R. H., Bennett, A. F., and Sunnucks, P. (2013). Limited population structure, genetic drift and bottlenecks characterise an endangered bird species in a dynamic, fire-prone ecosystem. *PLoS One* 8:e59732. doi: 10.1371/journal.pone.0059732

Burbidge, A. H., Joseph, L., Toon, A., White, L. C., McGuire, A., and Austin, J. J. (2017). A case for realigning species limits in the southern Australian whipbirds long recognised as the Western Whipbird (*Psophodes nigrogularis*). *Emu* 117, 254–263. doi: 10.1080/01584197.2017.1313685

Burch, J. (2020). Parish plans as a source of evidence of Aboriginal land use in the Mallee back country. *Provenance J. Public Rec. Office Vic.* 18, 9–21.

Callister, K. E., Griffioen, P. A., Avitabile, S. C., Haslem, A., Kelly, L. T., Nimmo, D. G., et al. (2016). Historical maps from modern images: using remote sensing to model and map century-long vegetation change in a fire-prone region. *PLoS One* 11:e0150808. doi: 10.1371/journal.pone.0150808

Cheal, D. (2009). Twenty years of grazing reduction in semi-arid woodlands. *Pacific Cons. Biol.* 15, 268–277. doi: 10.1071/pc090268

Cheal, D. (2010). *Growth Stages and Tolerable Fire Intervals for Victoria's Native Vegetation Data Sets. Fire and Adaptive Management Report No. 84*. East Melbourne, VIC: Department of Sustainability and Environment.

Cheal, D. C., and Parkes, D. M. (1989). "Mallee vegetation in Victoria," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Victoria, VIC: CSIRO Publishing), 125–140.

Cheal, P., Day, J. C., and Meredith, C. (1979). *Fire in the National Parks of North-West Victoria*. Melbourne, VIC: National Parks Service.

Chuvieco, E., Giglio, L., and Justice, C. (2008). Global characterization of fire activity: towards defining fire regimes from Earth observation data. *Glob. Change Biol.* 14, 1488–1502. doi: 10.1111/j.1365-2486.2008.01585.x

Clarke, J. M., Grose, M., Thatcher, M., Round, V., and Heady, C. (2019). *Mallee Climate Projections 2019*. Melbourne, VIC: CSIRO.

Clarke, M. F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildl. Res.* 35, 385–394. doi: 10.1071/wr07137

Clarke, M. F., Avitabile, S. C., Brown, L., Callister, K. E., Haslem, A., Holland, G. J., et al. (2010). Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Aust. J. Bot.* 58, 363–372. doi: 10.1071/bt10051

Clarke, P. A. (2009). "Aboriginal culture and the Riverine environment," in *The Natural History of the Riverland and Murraylands*, ed. J. T. Jennings (Adelaide: Royal Society of South Australia), 142–161.

Clarke, P. J., Lawes, M. J., Murphy, B. P., Russell-Smith, J., Nano, C. E. M., Bradstock, R., et al. (2015). A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Sci. Total Environ.* 534, 31–42. doi: 10.1016/j.scitotenv.2015.04.002

Cogger, H. G. (1989). "Herpetofauna," in *Mediterranean Landscapes in Australia. Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Melbourne, VIC: CSIRO Publishing), 250–265.

Cohn, J. S., and Bradstock, R. A. (2000). Factors affecting post-fire seedling establishment of selected mallee understorey species. *Aust. J. Bot.* 48, 59–70. doi: 10.1071/bt98031

Cohn, J. S., Bradstock, R. A., and Burke, S. (2002). Effects of time-since-fire, topography and resprouting eucalypts on ephemeral understorey species composition, in semi-arid Mallee communities in western NSW. *Cunninghamia* 7, 579–600.

Connell, J., Hall, M., Nimmo, D., Watson, S. J., and Clarke, M. F. (2021). Fire, drought and flooding rains: the effect of climatic extremes on bird species' responses to time since fire. *Divers. Distrib.* (in press).

Cruz, M. G., McCaw, W. L., Anderson, W. R., and Gould, J. S. (2013). Fire behaviour modelling in semi-arid mallee-heath shrublands of southern Australia. *Environ. Modell. Softw.* 40, 21–34. doi: 10.1016/j.envsoft.2012.07.003

Cullen, L. E., and Grierson, P. F. (2009). Multi-decadal scale variability in autumn-winter rainfall in south-western Australia since 1655 AD as reconstructed from tree rings of *Callitris columellaris*. *Clim. Dyn.* 33, 433–444. doi: 10.1007/s00382-008-0457-8

Davis, H., Richie, E. G., Avitabile, S., Doherty, T., and Nimmo, D. G. (2018). Testing the assumptions of the pyrodiversity begets biodiversity hypothesis for termites in semi-arid Australia. *R. Soc. Open Sci.* 5:1725055. doi: 10.1098/rsos.172055

Department for Environment and Water (2016). *Last Bushfire and Prescribed Burn Boundaries*. Available online at: https://data.sa.gov.au/data/dataset/last-fire (accessed on December 2020).

Department of Environment Land Water and Planning (2020). *Fire History Last Burnt*. Available online at: http://services.land.vic.gov.au/catalogue/metadata?anzlicId=ANZVI0803004774&publicId=guest&extractionProviderId=1#tab1 (accessed on December 2020)

Department of Sustainability Environment Water Population and Communities (2013). *Interim Biogeographic Regionalisation for Australia (IBRA), Version 7*.

Department of the Environment (2018). *Major Vegetation Groups. National Vegetation Information System, Version 6*.

Dodson, J. (1982). "Current status of mallee ecosystems," in *Threats to Mallee in New South Wales*, ed. J. A. Mabutt (Sydney, NSW: Department of Environment and Planning), 17–33.

Doherty, T. S., Dickman, C. R., Nimmo, D. G., and Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biol. Cons.* 190, 60–68. doi: 10.1016/j.biocon.2015.05.013

Dowdy, A. J. (2020). Climatology of thunderstorms, convective rainfall and dry lightning environments in Australia. *Clim. Dyn.* 54, 3041–3052. doi: 10.1007/s00382-020-05167-9

Driscoll, D. A., Armenteras, D., Bennett, A. F., Brotons, L., Clarke, M. F., Doherty, T. S., et al. (2021). How fire interacts with habitat loss and fragmentation. *Biol. Rev.* 96, 976–998.

Driscoll, D. A., Smith, A. L., Blight, S., and Maindonald, J. (2012). Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiv. Cons.* 21, 1607–1625. doi: 10.1007/s10531-012-0267-5

Driscoll, D. A., Smith, A. L., Blight, S., and Sellar, I. (2020). Interactions among body size, trophic level and dispersal traits predict beetle detectability and occurrence responses to fire. *Ecol. Entom.* 45, 300–310. doi: 10.1111/een.12798

Driscoll, D. A., and Weir, T. (2005). Beetle responses to habitat fragmentation depend on ecological traits, remnant condition and shape. *Conserv. Biol.* 19, 182–194. doi: 10.1111/j.1523-1739.2005.00586.x

Eldridge, D. J., and James, A. I. (2009). Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecol. Manage. Rest.* 4, 114–119.

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., and Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front. Ecol. Environ.* 13:265–272. doi: 10.1890/140231

Farnsworth, L. M., Nimmo, D. G., Kelly, L. T., Bennett, A. F., and Clarke, M. F. (2014). Does pyrodiversity beget alpha, beta or gamma diversity? A case study using reptiles from semi-arid Australia. *Divers. Distrib.* 20, 663–673. doi: 10.1111/ddi.12181

Florentine, S., Milberg, P., Di Stefano, J., Westbrooke, M., and Graz, P. (2015). Decade-long response of arid-land mallee vegetation to fire, flooding and grazing in south-eastern Australia. *J. Arid Environ.* 121, 7–14. doi: 10.1016/j.jaridenv.2015.05.006

Friend, G. R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biol. Cons.* 65, 99–114. doi: 10.1016/0006-3207(93)90439-8

Friend, G. R., and Williams, M. R. (1996). Impact of fire on invertebrate communities in mallee-heath shrublands of southwestern Australia. *Pac. Cons. Biol.* 2, 244–267. doi: 10.1071/pc960244

Geary, W., Ritchie, E. G., Lawton, J. A., Healey, T. R., and Nimmo, D. G. (2018). Incorporating disturbance into trophic ecology: fire history shapes mesopredator suppression by an apex predator. *J. Appl. Ecol.* 55, 1594–1603. doi: 10.1111/1365-2664.13125

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T., and Ritchie, E. G. (2020). Predator responses to fire: a global systematic review and meta-analysis. *J. Anim. Ecol.* 89, 955–971. doi: 10.1111/1365-2656.13153

Geiser, F., Stawski, C., Wacker, C. B., and Nowack, J. (2017). Phoenix from the ashes: fire, torpor, and the evolution of mammalian endothermy. *Front. Physiol.* 8:842. doi: 10.3389/fphys.2017.00842

Gibson, R., Bradstock, R., Penman, T., and Driscoll, D. A. (2014). Changing dominance of key plant species across a Mediterranean climate region; implications for fuel types and future fire regimes. *Plant Ecol.* 215, 83–95. doi: 10.1007/s11258-013-0280-0

Gibson, R., Bradstock, R., Penman, T., Keith, D. A., and Driscoll, D. A. (2015). Climatic, vegetation and edaphic influences on the probability of fire across Mediterranean woodlands of south eastern Australia. *J. Biogeog.* 42, 1750–1760. doi: 10.1111/jbi.12547

Giljohann, K. M., Kelly, L. T., Connell, J., Clarke, M. F., Clarke, R. H., Regan, T. R., et al. (2017a). Assessing the sensitivity of biodiversity indices used to inform fire management. *J. Appl. Ecol.* 55, 461–471. doi: 10.1111/1365-2664.13006

Giljohann, K. M., McCarthy, M. A., Keith, D. A., Kelly, L. T., Tozer, M. G., and Regan, T. J. (2017b). Interactions between rainfall, fire and herbivory drive resprouter vital rates in a semi-arid ecosystem. *J. Ecol.* 105, 1562–1570. doi: 10.1111/1365-2745.12768

Gosper, C. R., Prober, S. M., and Yates, C. J. (2013). Estimating fire interval bounds using vital attributes: Implications of uncertainty and among-population variability. *Ecol. Appl.* 23, 924–935. doi: 10.1890/12-0621.1

Gosper, C. R., Yates, C. J., and Prober, S. M. (2012a). Changes in plant species and functional composition with time since fire in two mediterranean climate plant communities. *J. Veg. Sci.* 23, 1071–1081. doi: 10.1111/j.1654-1103.2012.01434.x

Gosper, C. R., Yates, C. J., Prober, S. M., and Parsons, B. C. (2012b). Contrasting changes in vegetation structure and diversity with time since fire in two Australian Mediterranean-climate plant communities. *Aust. Ecol.* 37, 164–174. doi: 10.1111/j.1442-9993.2011.02259.x

Gullan, P. J., Cranston, P. S., and Cook, L. G. (1997). The response of gall-inducing scale insects (Hemiptera: Eriococcidae: Apiomorpha Rubsaamen) to the fire history of mallee eucalypts in Danggali Conservation Park, South Australia. *Trans. R. Soc. South Aust.* 121, 137–146.

Haslem, A., Avitabile, S. C., Taylor, R. S., Kelly, L. T., Watson, S. J., Nimmo, D. G., et al. (2012). Time-since-fire and inter-fire interval influence hollow availability for fauna in a fire-prone system. *Biol. Conserv.* 152, 212–221. doi: 10.1016/j.biocon.2012.04.007

Haslem, A., Callister, K. E., Avitabile, S. C., Griffioen, P. A., Kelly, L. T., Nimmo, D. G., et al. (2010). A framework for mapping vegetation over broad spatial extents: a technique to aid land management across jurisdictional boundaries. *Landscape Urban Plan.* 97, 296–305. doi: 10.1016/j.landurbplan.2010.07.002

Haslem, A., Kelly, L. T., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., et al. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *J. Appl. Ecol.* 48, 247–256. doi: 10.1111/j.1365-2664.2010.01906.x

Hayward, M. W., Ward-Fear, G., L'Hotellier, F., Herman, K., Kabat, A. P., and Gibbons, J. P. (2016). Could biodiversity loss have increased Australia's bushfire threat? *Anim. Cons.* 19, 490–497. doi: 10.1111/acv.12269

He, T., Lamont, B. B., and Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biol. Rev.* 94, 1983–2010. doi: 10.1111/brv.12544

Hill, K. D. (1989). "Mallee eucalypt communities: their classification and biogeography," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and Their Management*, eds J. C. Noble and R. A. Bradstock (Melbourne, VIC: CSIRO Publishing), 93–108.

Hradsky, B. A. (2020). Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildl. Res.* 47, 1–15. doi: 10.1071/wr19027

Hunter, D. O., Lagisz, M., Leo, V., Nakagawa, S., and Letnic, M. (2018). Not all predators are equal: a continent-scale analysis of the effects of predator control on Australian mammals. *Mamm. Rev.* 48, 108–122. doi: 10.1111/mam.12115

James, C. D., Landsberg, J., and Morton, S. R. (1999). Provision of watering points in the Australian arid zone: a review of effects on biota. *J. Arid Env.* 41, 87–121. doi: 10.1006/jare.1998.0467

Keast, A. (1968). Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu* 67, 159–209. doi: 10.1071/mu967159

Keeley, J. E. (1986). "Resilience of Mediterranean shrub communities to fires," in *Resilience in Mediterranean-Type Ecosystems*, eds D. Bell, A. J. M. Hopkins, and B. B. Lamont (Dordrecht: DrW Junk), 95–112. doi: 10.1007/978-94-009-4822-8_7

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., and Rundel, P. W. (2012). *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge: Cambridge University Press.

Keeley, J. E., Fotheringham, C. J., and Baer-Keeley, M. (2005). Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecol. Appl.* 15, 1515–1534. doi: 10.1890/04-1005

Keith, D. A. (2012). "Functional traits: their roles in understanding and predicting biotic responses to fire regimes from individuals to landscapes," in *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World*, eds R. A. Bradstock, A. M. Gill, and R. J. Williams (Collingwood: CSIRO Publishing), 97–125.

Keith, D. A., and Tozer, M. G. (2012). The influence of fire, herbivores and rainfall on vegetation dynamics in the mallee: a long-term experiment. *Proc. Linn. Soc. NSW* 134, A39–A54.

Kelly, L. T., Bennett, A. F., Clarke, M. F., and McCarthy, M. A. (2015). Optimal fire histories for biodiversity conservation. *Conserv. Biol.* 29, 473–481. doi: 10.1111/cobi.12384

Kelly, L. T., Dayman, R., Nimmo, D. G., Clarke, M. F., and Bennett, A. F. (2013). Spatial and temporal drivers of small mammal distributions in a semi-arid environment: the role of rainfall, vegetation and life-history. *Aust. Ecol.* 38, 786–797. doi: 10.1111/aec.12018

Kelly, L. T., Giljohann, K. M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., et al. (2020). Fire and biodiversity in the Anthropocene. *Science* 370:eabb0355. doi: 10.1126/science.abb0355

Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Clarke, M. F., and Bennett, A. F. (2010). The short-term responses of small mammals to wildfire in semiarid mallee shrubland, Australia. *Wildl. Res.* 37, 293–300. doi: 10.1071/wr10016

Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Haslem, A., Watson, S. J., Clarke, M. F., et al. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Divers. Distrib.* 17, 462–473. doi: 10.1111/j.1472-4642.2011.00754.x

Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Taylor, R. S., Watson, S. J., Clarke, M. F., et al. (2012). Managing fire mosaics for small mammal conservation: a landscape perspective. *J. Appl. Ecol.* 49, 412–421. doi: 10.1111/j.1365-2664.2012.02124.x

Kenny, S. A., Bennett, A. F., Clarke, M. F., and Morgan, J. W. (2018). Time-since-fire and climate interact to affect the structural recovery of an Australian semi-arid plant community. *Austral. Ecol.* 43, 456–469. doi: 10.1111/aec.12582

Koch, P. J. (2015). *Habitat 141 Landscape Conservation Action Plan. Summary Report. Unpublished Report for the Habitat 141 Alliance*. Brisbane: Greening Australia.

Leblanc, M., Tweed, S., Van Dijk, A., and Timbal, B. (2012). A review of historic and future hydrological changes in the Murray-Darling Basin. *Glob. Planet Change* 80-81, 226–246. doi: 10.1016/j.gloplacha.2011.10.012

Leonard, S., Bennett, A. F., and Clarke, M. F. (2014). Determinants of the occurrence of unburnt patches: potential biotic refuges in a large intense wildfire in south-eastern Australia. *For. Ecol. Manag.* 314, 85–93. doi: 10.1016/j.foreco.2013.11.036

Letnic, M., Dickman, C. R., Tischler, M. K., Tamayo, B., and Beh, C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *J. Arid Environ.* 59, 85–114. doi: 10.1016/j.jaridenv.2004.01.014

Letnic, M., Koch, F., Gordon, C., Crowther, M. S., and Dickman, C. R. (2009). Keystone effects of an alien top predator stem extinctions of native mammals. *Proc. R. Soc. B* 276, 3249–3256. doi: 10.1098/rspb.2009.0574

Letnic, M., Ritchie, E. G., and Dickman, C. R. (2012). Top predators as biodiversity regulators: the dingo *Canis lupus* dingo as a case study. *Biol. Rev.* 87, 390–413. doi: 10.1111/j.1469-185x.2011.00203.x

Long, M. (2006). A climatology of extreme fire weather days in Victoria. *Aust. Meteor. Mag.* 55, 3–18.

Ludwig, J. A., Macleod, N. D., and Noble, J. C. (1990). "An expert system for fire management in mallee reserves," in *The Mallee Lands – a Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (East Melbourne, VIC: CSIRO Publishing), 214–217.

Luke, R. H., and McArthur, A. G. (1978). *Bushfires in Australia*. Canberra, VIC: Australian Government Publishing Service.

Lumsden, L., Nelson, J., and Lindeman, M. (2008). *Ecological Research on the Eastern Long-eared Bat Nyctophilus timoriensis (South-Eastern Form). A Report to the Mallee Catchment Management Authority*. Heidelberg, VIC: Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment.

Mariani, M., Holz, A., Veblen, T. T., Williamson, G., Fletcher, M.-S., and Bowman, D. M. J. S. (2018). Climate change amplifications of climate-fire teleconnections in the Southern Hemisphere. *Geophys. Res. Lett.* 45, 5071–5081. doi: 10.1029/2018gl078294

McCaw, W. L. (1997). *Predicting Fire Spread in Western Australian Mallee-Heath Shrubland*. PhD thesis. Sydney, NSW: University of New South Wales.

Menkhorst, P. W., and Bennett, A. F. (1990). "Vertebrate fauna of mallee vegetation in southern Australia," in *The Mallee Lands: A Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (East Melbourne, VIC: CSIRO Publishing), 39–53.

Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R., et al. (2011). A fresh framework for the ecology of arid Australia. *J. Arid Environ.* 75, 313–329. doi: 10.1016/j.jaridenv.2010.11.001

National Parks and Wildlife Service (2020). *NPWS Fire History - Wildfires and Prescribed Burns*. Available online at: https://data.gov.au/dataset/ds-nsw-1f694774-49d5-47b8-8dd0-77ca8376eb04/details?q= (accessed on December 2020).

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., et al. (2019). Animal movements in fire-prone landscapes. *Biol. Rev.* 94, 981–998.

Nimmo, D. G., Kelly, L. T., Farnsworth, L. M., Watson, S. J., and Bennett, A. F. (2014). Why do some species have geographically varying responses to fire history? *Ecography* 37, 805–813. doi: 10.1111/ecog.00684

Nimmo, D. G., Kelly, L. T., Spence-Bailey, L. M., Watson, S. J., Haslem, A., White, J. G., et al. (2012). Predicting the century-long post-fire responses of reptiles. *Glob. Ecol. Biogeog.* 21, 1062–1073. doi: 10.1111/j.1466-8238.2011.00747.x

Nimmo, D. G., Kelly, L. T., Spence-Bailey, L. M., Watson, S. J., Taylor, R. S., Clarke, M. F., et al. (2013). Fire mosaics and reptile conservation in a fire-prone region. *Cons. Biol.* 159, 248–256.

Noble, J., and Vines, R. (1993). Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: grass fuel dynamics and associated weather patterns. *Rangeland J.* 15, 270–297. doi: 10.1071/rj9930270

Noble, J. C. (2001). Lignotubers and meristem dependence in mallee (*Eucalyptus* spp.) coppicing after fire. *Aust. J. Bot.* 49, 31–41.

Noble, J. C., and Bradstock, R. A. (eds) (1989). *Mediterranean Landscapes in Australia: Mallee Ecosystems and Their Management*. Melbourne, VIC: CSIRO Publishing.

Noble, J. C., Joss, P. J., and Jones, G. K. (eds) (1990). *The Mallee Lands: A Conservation Perspective*. East Melbourne, VIC: CSIRO Publications.

Noble, J. C., and Kimber, R. G. (1997). On the ethnoecology of mallee root-water. *Aborig. Hist.* 21, 170–202.

Noble, J. C., Smith, A. W., and Leslie, H. W. (1980). Fire in the mallee shrublands of western New South Wales. *Aust. Rangel. J.* 2, 104–114. doi: 10.1071/rj9800104

O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2011a). Climatic anomalies drive wildfire occurrence and extent in semi-arid shrublands and woodlands of southwest Australia. *Ecosphere* 2, 1–15.

O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2011b). Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. *J. Biogeogr.* 38, 112–124. doi: 10.1111/j.1365-2699.2010.02381.x

O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2014). Scale-dependent thresholds in the dominant controls of wildfire size in semi-arid southwest Australia. *Ecosphere* 5:93.

Parkes, D. M., and Cheal, D. C. (1990). "Perceptions of mallee vegetation," in *The Mallee Lands: A Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (East Melbourne, VIC: CSIRO Publications), 3–7.

Parr, C. L., and Andersen, A. N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Cons. Biol.* 20, 1610–1619. doi: 10.1111/j.1523-1739.2006.00492.x

Parsons, B. C., and Gosper, C. R. (2011). Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. *Int. J. Wild. Fire* 20, 184–194. doi: 10.1071/wf09099

Parsons, R. F., and Rowan, J. N. (1968). Edaphic range and cohabitation of some mallee eucalypts in south-eastern Australia. *Aust. J. Bot.* 16, 109–116. doi: 10.1071/bt9680109

Paton, D. C. (1980). The importance of manna, honeydew and lerp in the diet of honeyeaters. *Emu* 80, 213–226. doi: 10.1080/01584197.1980.11799277

Pausas, J. G., and Bradstock, R. A. (2007). Fire persistence traits of plants along a productivity and disturbance gradient in Mediterranean shrublands of south-east Australia. *Glob. Ecol. Biogeogr.* 16, 330–340. doi: 10.1111/j.1466-8238.2006.00283.x

Pell, S. D., Chivas, A. R., and Williams, I. S. (2001). The Mallee Dunefield: development and sand provenance. *J. Arid Environ.* 48, 149–170. doi: 10.1006/jare.2000.0751

Pianka, E. R. (1969). Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50, 498–502. doi: 10.2307/1933908

Pickett, S. T. A., Collins, S. L., and Armesto, J. J. (1987). Models, mechanisms and pathways of succession. *Bot. Rev.* 53, 335–371. doi: 10.1007/bf02858321

Pollock, L. J., Kelly, L. T., Thomas, F. M., Soe, P., Morris, W. K., White, M., et al. (2018). Combining functional traits, the environment and multiple surveys to understand semi-arid tree distributions. *J. Veg. Sci.* 29, 967–977. doi: 10.1111/jvs.12686

Prober, S. M., Yuen, E., O'Connor, M. H., and Schultz, L. (2016). Ngadju kala: Australian Aboriginal fire knowledge in the Great Western Woodlands. *Austral. Ecol.* 41, 716–732. doi: 10.1111/aec.12377

Rainsford, F. W., Kelly, L. T., Leonard, S. W. J., and Bennett, A. F. (2020). Post-fire development of faunal habitat depends on plant regeneration traits. *Austral. Ecol.* 45, 800–812.

Read, J. L., Firn, J., Grice, A. C., Murphy, R., Ryan-Colton, E., and Schlesinger, C. A. (2020). Ranking buffel: comparative risk and mitigation costs of key environmental and socio-cultural threats in central Australia. *Ecol. Evol.* 10, 12745–12763. doi: 10.1002/ece3.6724

Richards, T., Pavlides, C., Walshe, K., Webber, H., and Johnston, R. (2007). Box Gully: new evidence for Aboriginal occupation of Australia south of the Murray River prior to the last glacial maximum. *Arch. Ocean.* 42, 1–11. doi: 10.1002/j.1834-4453.2007.tb00001.x

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G., and McDonald, R. A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.* 27, 265–271. doi: 10.1016/j.tree.2012.01.001

Ross, A. (1981). Holocene environments and prehistoric site patterning in the Victorian mallee. *Arch. Ocean.* 16, 145–155. doi: 10.1002/j.1834-4453.1981.tb00025.x

Sandell, P. (2006). Promoting woodland recovery in the Victorian mallee parks. *Proc. R. Soc. Vict.* 118, 313–321.

Sandell, P., Tolhurst, K. G., Dalton, J., Scott, B., and Smith, M. (2006). Fire management prescriptions for the Victorian Mallee Parks. *Proc. R. Soc. Vic.* 118, 395–412.

Schlesinger, C. A., Noble, I. R., and Weir, T. (1997). Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: reptile and beetle populations in sites of differing fire history. *Rangelands J.* 19, 190–205. doi: 10.1071/rj9970190

Schodde, R. (1981). "Bird communities of the Australian mallee: composition, derivation, distribution, structure and seasonal cycles," in *Ecosystems of the World. II Mediterranean-Type Shrublands*, eds F. di Castri, D. W. Goodall, and R. L. Specht (Amsterdam: Elsevier), 387–415.

Schodde, R. (1990). "The bird fauna of the mallee - its biogeography and future," in *The Mallee Lands: a Conservation Perspective*, eds J. C. Noble, P. J. Joss, and G. K. Jones (Melbourne, VIC: CSIRO), 61–70.

Schodde, R., and Mason, I. J. (1999). *The Directory of Australian Birds - Passerines: A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and its Territories*. Collingwood: CSIRO Publishing.

Selwood, K. E., Cunningham, S. C., and Mac Nally, R. (2019). Beyond refuges: identifying temporally dynamic havens to support ecological resistance and resilience to climatic disturbances. *Biol. Cons.* 233, 131–138. doi: 10.1016/j.biocon.2019.02.034

Senior, K. L., Giljohann, K. M., McCarthy, M. A., Rainsford, F. W., and Kelly, L. T. (2021). Predicting mammal responses to pyrodiversity: from microbats to macropods. *Biol. Conserv.* 256:109031. doi: 10.1016/j.biocon.2021.109031

Simms, A., Scott, M., Watson, S., and Leonard, S. (2019). Attenuated post-fire fauna succession: the effects of surrounding landscape context on post-fire colonisation of fauna. *Wildl. Res.* 46, 247–255. doi: 10.1071/wr18131

Smith, A., Avitabile, S. C., and Leonard, S. W. J. (2017). Less fuel for the fire: malleefowl (*Leipoa ocellata*) nesting activity affects fuel loads and fire behaviour. *Wildl. Res.* 43, 640–648. doi: 10.1071/wr16127

Smith, A. L., Bull, C. M., and Driscoll, D. A. (2013). Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression. *J. Appl. Ecol.* 50, 1178–1186. doi: 10.1111/1365-2664.12119

Smith, A. L., Landguth, E. L., Bull, C. M., Banks, S. C., Gardner, M. G., and Driscoll, D. A. (2016). Dispersal responses override density effects on genetic diversity during post-disturbance succession. *Proc. R. Soc. B: Biol. Sci.* 283, 20152934. doi: 10.1098/rspb.2015.2934

Smith, W., Neale, T., and Weir, J. K. (2021). Persuasion without policies: the work of reviving Indigenous peoples' fire management in southern Australia. *Geoforum* 120, 82–92. doi: 10.1016/j.geoforum.2021.01.015

Sparrow, A. (1989). "Mallee vegetation in South Australia," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Victoria, VIC: CSIRO Publishing), 109–124.

Speer, M. S. (2013). Dust storm frequency and impact over eastern Australia determined by state of Pacific climate system. *Weather Clim. Extremes* 2, 16–21. doi: 10.1016/j.wace.2013.10.004

Taylor, R. S., Watson, S. J., Nimmo, D. G., Kelly, L. T., Bennett, A. F., and Clarke, M. F. (2012). Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Divers. Distrib.* 18, 519–529. doi: 10.1111/j.1472-4642.2011.00842.x

Teasedale, L. C., Smith, A. L., Thomas, M., Whitehead, C. A., and Driscoll, D. A. (2013). Detecting invertebrate responses to fire depends on sampling method and taxonomic resolution. *Aust. Ecol.* 38, 874–883. doi: 10.1111/aec.12024

Travers, S. K., and Eldridge, D. J. (2013). Increased rainfall frequency triggers an increase in litter fall rates of reproductive structures in an arid eucalypt woodland. *Aust. Ecol.* 38, 820–830. doi: 10.1111/aec.12055

Tyson, M., Vaillancourt, R. E., and Reid, J. B. (1998). Determination of clone size and age in a mallee eucalypt using RAPDs. *Aust. J. Bot.* 46, 161–172. doi: 10.1071/bt97003

Verdon, S. J., Watson, S. J., and Clarke, M. F. (2019). Modelling variability in the fire response of an endangered bird to improve fire-management. *Ecol. Appl.* 29, e01980. doi: 10.1002/eap.1980

Verdon, S. J., Watson, S. J., Nimmo, D. G., and Clarke, M. F. (2020). Are all fauna associated with the same structural features of the foundation species *Triodia scariosa*? *Austral Ecol.* 45, 773–787.

Victorian Traditional Owner Cultural Fire Knowledge and Group (2019). *The Victorian Traditional Owner Cultural Fire Strategy*. Melbourne, VIC: Federation of Victorian Traditional Owner Corporations, Department of Environment, Water and Planning, Parks Victoria, Country Fire Authority.

Wasson, R. J. (1989). "Landforms," in *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*, eds J. C. Noble and R. A. Bradstock (Victoria, VIC: CSIRO Publishing), 13–34.

Watson, S. J., Taylor, R. S., Nimmo, D. G., Kelly, L. T., Clarke, M. F., and Bennett, A. F. (2012a). The influence of unburnt patches and distance from refuges on post-fire bird communities. *Anim. Conserv.* 15, 499–507.

Watson, S. J., Taylor, R. S., Nimmo, D. G., Kelly, L. T., Haslem, A., Clarke, M. F., et al. (2012b). Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? *Ecol. Appl.* 22, 685–696.

Wellington, A. B., and Noble, I. R. (1985). Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *J. Ecol.* 73, 645–656.

Westbrooke, M. E., and Florentine, S. K. (2005). Rainfall-driven episodic flood events: are they a major factor in moulding New South Wales arid land vegetation patterns? *Aust. Geog.* 36, 171–181.

White, M., Oates, A., Barlow, T., Pelikan, M., Brown, J., Rosengren, N., et al. (2003). *The Vegetation of North-West Victoria: a Report to the Wimmera, North Central and Mallee Catchment Management Authorities*. Melbourne, VIC: Arthur Rylah Institute for Environmental Research.

White, M. D. (2006). The mallee vegetation of north western Victoria. *Proc. R. Soc. Vic.* 118, 229–243.

Wilson, A. D., Hodgkinson, K. C., and Noble, J. C. (1988). "Vegetation attributes and their application to the management of Australian rangelands," in *Vegetation Science Applications for Rangeland Analysis and Management*, ed. P. T. Tueller (Netherlands: Springer), 253–294.

Yates, C., Gosper, C., Hopper, S., Keith, D., Prober, S., and Tozer, M. (2017). "Mallee woodlands and shrublands: the mallee, muruk/muert and maalok vegetation of southern Australia," in *Australian Vegetation*, ed. D. Keith (Cambridge: Cambridge University Press), 570–598.

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Fire in Semi-Arid Shrublands and Woodlands: Spatial and Temporal Patterns in an Australian Landscape

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Semi-arid landscapes are of interest to fire ecologists because they are generally located in the climatic transition zone between arid lands (where fires tend to be rare due to lack of fuel, but are enhanced following large rainfall episodes) and more mesic regions (where fire activity tends to be enhanced following severe rainfall deficits). Here we report on the characteristics of the contemporary fire regimes operating in a semi-arid region of inland south-western Australia with rainfall averaging around 300 mm per annum. To characterize fire regimes, we analyzed a geodatabase of fire scars (1960–2018) to derive fire preferences for each major vegetation type and fire episode and used known fire intervals to model fire hazard over time and calculate typical fire frequencies. We also used super epoch analysis and correlations to explore relationships between annual fire extent and rainfall received before the fire. We found fires strongly favored sandplain shrublands, and these tended to experience hot crown fires once every 100 years (median fire interval), with fire hazard increasing linearly over time. In contrast, fires were rare in eucalypt woodland and other vegetation types, with a median interval of 870 years and broadly consistent fire hazard over time. Annual fire extent was most strongly linked with high rainfall in the year prior to fire, and this was particularly so for eucalypt woodlands. Large-scale fires in shrublands tended to favor areas burnt in previous large fires, whereas in woodlands they favored edges. In conclusion, we found divergent fire regimes across the major vegetation types of the region. Sandplain shrublands were similar to Mediterranean shrublands in that they experienced intense stand-replacing wildfires which recovered vigorously although slowly, meaning burnt shrublands did not experience fires again for at least 25 and 100 years on average. In contrast, eucalypt woodlands were fire sensitive (trees readily killed by fire) and experienced fires mostly around the edges, spreading into core areas only after large rainfall events elevated fuel levels. Overall, both vegetation types subscribed to typical arid-zone fire regimes where elevated rainfall, and not drought, promoted fires, although the role of fuel accumulation over time was more important in the shrublands.

Keywords: fire regime, spatial patterns, semi-arid, fire drivers, fire ecology

INTRODUCTION

Fire influences the composition and function of many ecosystems across the globe (He et al., 2019). It is generally accepted that the biota of these ecosystems have become adapted to natural fire regimes over millennia, and any major deviations from this regime will likely influence their composition, structure and/or functioning (Bowman et al., 2009; Avitabile et al., 2013). Effectively managing fire within terrestrial ecosystems thus relies on knowledge of both past and present fire regimes. Understanding fire regimes can also help fire managers predict future fire behavior, manage fuels and fire risks, and plan and implement appropriate fire intervals and fire age distributions for biodiversity conservation (Driscoll et al., 2010).

Both historic and contemporary fire regimes are poorly known for many ecosystems, especially so for large, remote, and sparsely populated regions, which includes large expanses of the world's drylands. Fire is a relatively rare event in arid lands because rainfall and productivity are too low to support the dense vegetation and continuous fuel needed to sustain regular fires (Pausas and Bradstock, 2007; Pausas and Ribeiro, 2013). There are exceptions to this though, such as landscapes dominated by xerophytic perennial grasses (e.g., *Triodia* grasslands in arid Australia), areas lower in the landscape which develop denser vegetation, periods of unusually high rainfall which result in exceptional grass and forb growth, or landscapes where invasive species, particularly alien grasses, enhance fuel loads (Allan and Southgate, 2002; Keeley et al., 2012; Balch et al., 2013; van Etten and Burrows, 2018).

Semi-arid zones occur in the transition between mesic regions where fire regimes are typically driven by occasional droughts that render vegetation more flammable -and arid lands where fire regimes are typically driven by rainfall-enhanced fuels resulting from rare high rainfall events (Pausas and Paula, 2012; McLauchlan et al., 2020). These drivers tend to unfold once sufficient vegetation recovery after fire has occurred, although fuel accumulation can continue for decades after recovery in some ecosystems, and so time since fire (TSF) can continue to shape fire hazard, whilst in other ecosystems fire weather plays a more important role, post-recovery (Moritz et al., 2004). Semi-arid zones, given sufficient TSF, can support shrub-dominated vegetation dense enough to enable crown fires, which are typically intense and "stand-replacing" (Keeley et al., 2012; Dalgleish et al., 2015). However, they can also support more open vegetation which rarely experiences fire (Gosper et al., 2013a,b). In the western United States, McKenzie and Littell (2017) identified hybrid ecoregions in intermediate rainfall zones where both recent drought and abundant rainfall in previous years can encourage fires, but it is unclear if this due to temporal wet-dry sequences or spatial configurations of ecosystems with divergent fire regimes and drivers.

Across the transition from an arid to Mediterranean-type climate in southern Australia, fire frequency and extent increases in a southerly direction in line with increasing rainfall, productivity, and vegetation cover (Pausas and Bradstock, 2007). Gibson et al. (2015) also found increasing fire frequency with increasing rainfall across this gradient, but also greater influence of TSF driving fire intervals, although pre-fire rainfall was the most important driver across the whole gradient. They also found that fuel accumulation (i.e., TSF) was a more influential driver on more fertile patches of soil. This demonstrates the importance of productivity variation in explaining differences in fire regimes at both regional and landscape scales. Indeed, landscapes are not always uniform in terms of the spatial arrangement of fire regimes (as well as extent of individual fires), potentially varying from regularly burnt and highly fire-prone patches or vegetation types to areas that rarely or never experience fire, which reflects variation in topography, geomorphology and vegetation (Turner and Romme, 1994; Kane et al., 2015; McLauchlan et al., 2020).

Understanding the controls of fires at the landscape scale and why some areas are preferentially burnt over others, is important for both researchers and land managers (Archibald et al., 2009). Moreover, fine-scale patchiness in burn area and intensity may occur, even in the most fire-prone vegetation, contributing to heterogeneity of vegetation at this and broader spatial scales (Turner et al., 1994; Schoennagel et al., 2009). Such patchiness may arise from local-scale variation in vegetation and fuel, the residual effect(s) of previous fires, or may reflect stochastic factors related to fire behavior. The idea of ecological memory is important too, with burnt patches in the landscape potentially becoming preferred pathways for subsequent fires, which may then lead to further differentiation of landscape patterns over time (Peterson, 2002).

The main method used to map and analyze fire history from regional to landscape scales, involves manipulation, comparison and analysis of remotely sensed imagery to detect recently burnt areas. This imagery is typically obtained from satellites, which routinely became available from about 1972, and have improved in spectral range and resolution since then (Turner et al., 2008; Avitabile et al., 2013). To obtain fire scar information before this time requires interpretation of aerial photography, a methodology which suffers from intermittent coverage, variable quality and resolution, and narrow spectral range, although it is generally suitable for arid/semi-arid regions as fire scars are often detectable for many years before the vegetation fully regenerates (Burrows and Christensen, 1990). Although modeling reflectance data from satellite imagery to estimate long-term fire history is a promising approach for some ecosystems (Callister et al., 2016), fire mapping at regional scales is mostly limited to the last few decades. Once obtained, accurately mapped fire scars can be analyzed using GIS and statistical models to determine the key characteristics of fire regimes such as typical fire intervals (e.g., McCarthy et al., 2001), fire preferences (e.g., Moreira et al., 2009), and relationships with climate anomalies and other potential drivers (e.g., O'Donnell et al., 2011a).

In this paper, we analyzed mapped fire scars to quantify and describe the contemporary fire regimes of a poorly known area of inland, semi-arid Western Australia. The study area is covered by a complex mosaic of several distinct vegetation types, some of which are dense fire-prone shrublands, but others appear to be fire sensitive. Local land managers have been concerned over the size and frequency of recent fires (Braun, 2006; Parsons and Gosper, 2011). We use this case study to address broader ecological questions regarding landscape-scale fire preferences and regimes: (1) are spatial patterns of fire random or deterministic?; (2) how important are occasional large fires in shaping fire history and fire regimes?; (3) do landscapes with contrasting vegetation types have different fire regimes and, if so, how can they coexist?; and (4) are major fires in this semi-arid transition zone mostly driven by above- or below-average rainfall episodes, or some combination of these?

MATERIALS AND METHODS

Study Area

The study area covers ∼3,300 km^2 of the transitional zone between the Southwest Botanical Province of Western Australia (which has a Mediterranean-type climate) and the arid Eremean Botanical Province (**Figure 1**). It is located approximately 400 km north-east of Perth and the nearest coastline lies about 200 km to the west. Almost all fires are confined to the study area because it is bounded by large salt lakes to the east and west, the heavily cleared wheatbelt to the south, and more arid and sparse vegetation to the north (**Figure 1**). This study area is therefore ideal for studying fire patterns. It is also an area of high conservation value due to its high diversity of plant taxa (Hopper and Gioia, 2004) and high degree of intactness (i.e., uncleared and little modified by human activity).

The climate of the study area is semi-arid with average annual rainfall of *c.*300 mm, of which just over one third falls in cooler months (June to August inclusive), and an aridity index (ratio of average precipitation to potential evaporation) of approximately 0.15. A climatic gradient exists across the study area, running in a more-or-less north-easterly direction. Based on interpolated climate surfaces using rainfall data from 1976 to 2005 (ANUCLIM v6.1; Xu and Hutchinson, 2011), average annual rainfall declines gradually from 300 mm in south-west corner to 280 mm in the north-east corner, with the proportion of summer rain (January–March inclusive) increasing from 20 to 25%. Land tenure consists of vacant Crown land and destocked former pastoral leases, previously grazed by sheep (although lightly so in sandplain shrublands), but now mostly managed for conservation.

Vegetation of the study area comprises a mosaic of recurring vegetation types with 15 land systems described for the study area (Payne et al., 1998). These land systems have been grouped into five major land cover types as per recommendations of Payne et al. (1998), each having distinctive vegetation characteristics. These are hereafter called "vegetation types" in this paper and used as the basis for many of the analyses. These vegetation types are: (1) mulga woodland comprising *Acacia aneura* and other *Acacia* trees and tall shrubs on extensive hardpan plains and red loams, mostly found in northern parts of study area; (2) sandplain shrublands comprising dense shrub vegetation on gently undulating yellow sandplains derived from weathering of underlying granite and dominated by shrubs of *Acacia*, Myrtaceae (particularly *Melaleuca*), Proteaceae (e.g., *Hakea, Grevillea*), *Allocasuarina, Hibbertia* and Rutaceae (e.g., *Philotheca, Phebalium*); (3) more open tall shrublands of mixed species, but mostly *Acacia* and *Allocasuarina*, on ironstone and greenstone hills and rises; (4) eucalypt woodlands on alluvial plains and drainage lines dominated by york gum, *Eucalyptus loxophleba*, but also containing stands of salmon gum *E. salmonophloia* and gimlet *E. salubris*; and (5) salt lakes margins of fringing saltmarsh dominated by samphires, *Tecticornia* spp.

Of these vegetation types, we focus mostly on the sandplain shrublands, which correspond to the "Joseph" and "Bannar" land systems of Payne et al. (1998) and Beard et al.'s (2013) "tall shrubland thickets" (**Figure 1**), because it is by far the most

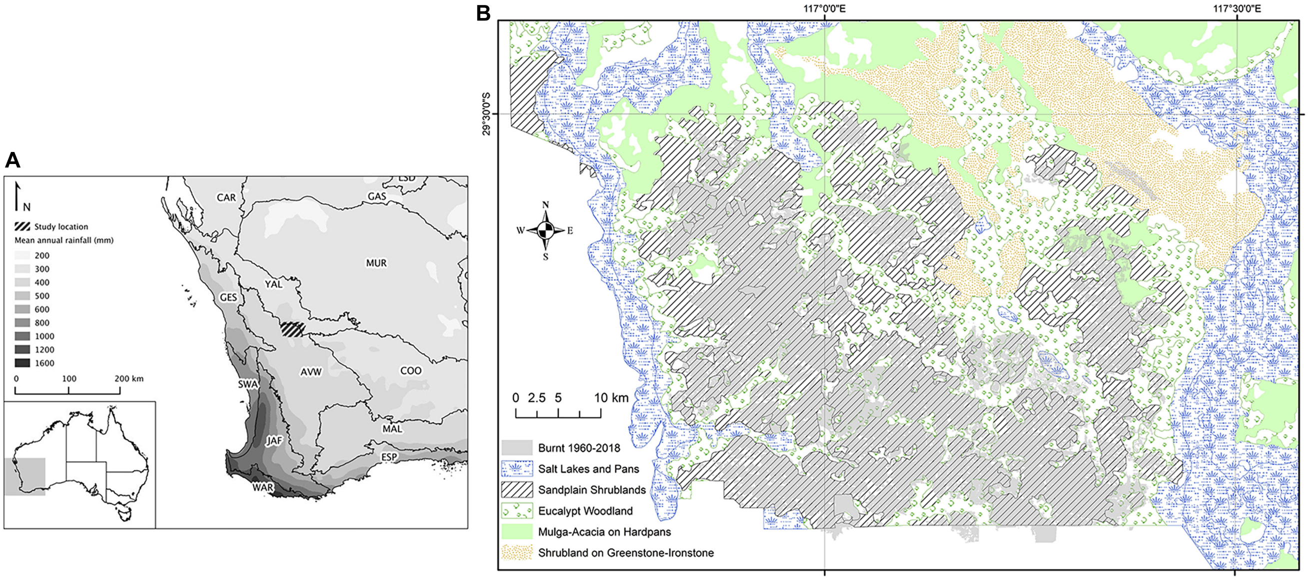

FIGURE 1 | Maps of study area showing: **(A)** location within Australia and region relative to average annual rainfall and Australian bioregions, and **(B)** areas burnt 1960–2018 (shaded in gray) in relation to major vegetation types as per legend.

widespread and most fire-prone, and as it has been well studied in terms of the effects of fire on various aspects of the biota (Doherty et al., 2015, 2017; Davis et al., 2016). Fires in this system tend to be intense crown fires that remove most of the available foliage and fuel, leaving only scorched larger stems (Braun, 2006; Dalgleish et al., 2015).

Fire-Scar Mapping

Existing digitized and geo-referenced fire mapping of the study area was obtained from several sources which used Landsat imagery and available aerial photographs to detect fire scars for the period 1969–2004 (Shu et al., 2004; Braun, 2006; Parsons and Gosper, 2011). These authors used a temporal sequence of satellite imagery (Landsat TM) consisting of annual summer images, supplemented with aerial photography taken in 1980 and 1969, with burnt areas identified by a dramatic change in reflectance between temporally successive images, with local knowledge used to distinguish fire events from other types of abrupt vegetation changes. For 2005–2018, a period of very few fires in the study area, we used a combination of MODIS burn area product (Boschetti et al., 2019) and Landsat TM imagery to manually digitize fire scars, and were also guided by reports from land managers on fire incidences and their burn boundaries. For 1960–1969, we used visual interpretation of available aerial photographs which covered at least part of study area (years 1959, 1960, 1962, 1968, and 1969) to map fires and estimate the year of fire based on degree of vegetation recovery (using later aerial photography with known fire dates as a guide to estimate vegetation recovery rates for the major vegetation types). Vegetation recovery after fire is typically very slow in the study area with fire scars evident for at least 10 years in most circumstances (O'Donnell et al., 2011b). To obtain the month when individual fires occurred, we used a combination of the Firewatch website[1] which displays monthly MODIS burned area maps, Landsat imagery via LandsatLook Viewer[2], and historical anecdotes; however month of fire for years prior to 1982 were uncertain due to lack of resolution and sufficient time sequences, and fires prior to 1972 (before satellite imagery became available) only within the nearest 0.5–2 years. We accept that the dates assigned to fire scars detected in the period 1950–1965 are particularly uncertain and that we may have missed some smaller fires in this period given the poor resolution of available aerial photography. However, we are confident that fires from 1960 to 2018 have been accurately mapped in space and are temporally accurate from 1968 and this facilitated the analysis of spatial extent and fire history, respectively. Digitized fire-scar mapping was thoroughly checked and field validated in this and previous studies (e.g., Parsons and Gosper, 2011; Dalgleish et al., 2015; Knuckey et al., 2016; Doherty et al., 2017).

Spatial Analyses

To assess landscape-scale fire preferences, we performed spatial intersections between mapped fire scars and the five broad vegetation types within a GIS (ArcGIS v10; ESRI, 2011). The spatial area of each intersection was calculated using the GIS and then compared to total area of each vegetation type available within the study area. All layers were reprojected to the same map projection and datum before spatial analyses.

To investigate whether individual fires preferentially burned certain vegetation types over others, we calculated selection ratios for each discrete fire event in the study area, except for a few very small fires and those occurring before 1970 as individual fire events could not be always distinguished from each other. This approach is based on habitat selection principles relating consumed to available resources (Manly et al., 1993), but has been applied to fire studies by comparing the proportion of different vegetation types in a burned area (consumed) to that of the burn and surrounding area (available) (Moreira et al., 2009; O'Donnell et al., 2011b). For a given vegetation type i, the selection ratio (w) is calculated as $w_i = o_i/\pi_i$ (Manly et al., 1993), where o_i is the proportion of the burned area covered by vegetation type i, and π_i is the proportion of available land in the burn area and surrounding buffer occupied by vegetation type i. If a given vegetation type is burnt in exact proportion to its availability, then $w = 1$. If the vegetation type is burnt more than expected by chance (i.e., preferentially), then $w > 1$. If the vegetation is burnt less than expected by chance (i.e., avoided), then $w < 1$. Different authors have used different sizes and shapes of buffers (which makes direct comparisons between studies difficult); however, for the purpose of this study we followed the advice of Oliveira et al. (2014) and made buffers approximately twice as large and the same shape as the burnt area of each fire. We did this by creating buffers of a width proportional to the size of the fire scar (varying from 0.3 km for small fires to 3.5 km for our largest fires) around the perimeter of each fire and then dissolving all separate buffers to create a single buffer in ArcGIS. Mean selection ratios of vegetation types were calculated and compared using one-way ANOVA. Selection ratios were also calculated for individual fires and episodes of several large wildfires (e.g., 2000–2002) to determine if they selectively favored previously burnt or unburnt areas. To determine if fires tended to favor areas closer to edge of vegetation type rather than toward their interior, the distance to nearest vegetation edge was calculated for 1,000 random points across the study area (using the proximity tool within GIS) and then means of such distances were compared between burnt and unburnt points using t-tests for each major vegetation type.

Relationships Between Fire Occurrence and Rainfall

We adapted a widely used statistical method for exploring relationships between time-series variables called superimposed epoch analysis (SEA; Chree, 1913) to determine associations between occurrence of fire(s) in a particular year and rainfall in corresponding and preceding years (Sherriff and Veblen, 2008; O'Donnell et al., 2011a). We used the financial year (FY) rather than calendar year in this analysis as this captured the main fire season (November to May) when most fires occurred and largest areas were burned. We firstly obtained monthly rainfall data

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[1] http://firewatch-pro.landgate.wa.gov.au/

[2] https://landsatlook.usgs.gov/

for nine evenly spaced points across the study area from SILO[3] which uses spatial interpolation of available weather station data to estimate monthly rainfall for each 0.05 degree grid cell. We then summed the monthly data for each FY and averaged the nine points to obtain the study area rainfall for each FY. We then calculated the average rainfall for FYs which recorded a fire, which we refer to as "fire years" (t_0; $n = 21$) and compared this to the overall mean FY rainfall for the region across the whole study period using standard (z-) scores and then z-tests to determine significance of anomalies in mean rainfall between fire years and all years. We then repeated the calculation of standard scores and test statistics for anomalies between the mean study area rainfall of successive years prior to fire years (t_{-1}, t_{-2} and t_{-3}) and the mean rainfall across all years, as well as for cumulative mean rainfall for current and previous years (up to 3 years prior to fire, with and without year of fire). We then repeated SEA to calculate (and test for) anomalies in mean rainfall for years of major fires ($n = 5$), and years of no fire ($n = 33$). Major fire years were defined as those with total annual burn area in excess of 50 km^2 which, although arbitrarily selected, corresponded to a clear break in the annual burn area distribution, with all "minor" fire years having less than 30 km^2 burnt. We used only rainfall and fire data for the period where fires could be confidently placed into a financial year (i.e., 1968–1969 to 2017–2018). In addition to SEA, we calculated Pearson's correlation coefficients between annual burn area and annual rainfall totals for year of fire, as well as rainfall for years prior to fire (single years and cumulative totals).

Fire Intervals

We used survival analysis to estimate and compare the fire intervals of the major vegetation types of the study area using the methodology developed by Johnson and Gutsell (1994) and McCarthy et al. (2001). Using 1,000 random point locations across the study area (with minimum allowed distance between points of 1 km to reduce potential for spatial autocorrelation), we interrogated the spatial data on fire history in the GIS; if the point had experienced two fires, we then calculated the bounded (uncensored) fire interval (in years and months); if only one fire had occurred we calculated two unbounded (censored) intervals (time since fire from current, and time to fire from 1950); if no fire occurred, we assumed an interval at least 65 years (censored). We decided to use both censored and uncensored intervals in the analyses to avoid underestimation of fire intervals given they are relatively long in our study area with large parts of the study area not burnt during the study period; this follows the approach used in other similar studies in southern semi-arid Australia (O'Donnell et al., 2011b; Gibson et al., 2015). This resulted in 923 intervals which included 489 for sandplain shrublands (10.9% of which were uncensored), and 292 for eucalypt woodland (2.2% uncensored). The remaining random points were in non-vegetation areas, e.g., salt lakes. Sufficient uncensored data was only available for these two major vegetation types to undertake survival analysis. We used random points rather than calculating intervals between individual fires due to the relatively low number of discrete fires and the difficulty in distinguishing between discrete fires, especially for some pre-1970 mapped scars and years when several large fires occurred (as other have done, e.g., Gibson et al., 2015; Rogeau et al., 2016).

From these intervals, we used the survreg function in R package "survival" (Diex, 2013) to fit Weibull curves to the data and provide maximum likelihood estimates of Weibull parameters for the two major vegetation types. We then converted these to Weibull equation parameters b and c, and calculated the median Weibull fire interval using MEI = $b(\ln 2)^{1/c}$ as per Moritz et al. (2004).

RESULTS

Landscape Fire Patterns

Of the five major types of vegetation found in the study area, fire has predominately occurred in the shrublands on sandplains (**Table 1** and **Figure 1**), with around two thirds of this vegetation type experiencing at least one fire from the early 1960s to the end of the study period in 2018. Some 20%

TABLE 1 | The total area and proportion of each major vegetation type of study area burnt in the period 1960–2018, and selection ratio for individual fires.

Major vegetation types	Area in km^2 (% of study area)	Area (km^2) burnt (% of total burnt area)	% of vegetation type burnt at least once	% of vegetation type burnt more than once	Selection ratio of individual fires (n) (±CI)
Mulga-*Acacia* woodland on hardpan plains and red loams	236.2 (6.4%)	12.5 (0.8%)	5.2	0.1	0.17^a (5) (±0.07)
Eucalyptus woodland on alluvial plains and drainage lines	1,008.3 (27.3%)	191.6 (12.2%)	17.6	1.4	0.34^a (21) (±0.11)
Mixed species-*Acacia* shrublands on yellow sandplains	1,548.0 (41.9%)	1,315.7 (83.6%)	65.1	19.8	1.37^c (24) (±0.15)
Acacia-Allocasuarina shrubland on greenstone-ironstone hills and rises	414.1 (11.2%)	50.9 (3.2%)	12.3	0	1.04^b (3) (±0.13)
Salt lakes and fringing saltmarsh	375.7 (10.2%)	4.1 (0.3%)	1.1	0	0.11^a (7) (±0.10)
Total (all veg types in study area)	3,694.7 (100%)	1,574.4 (100%)	34.3	8.5	–

Selection ratios are arithmetic means for 26 individual fires with number of fires (n) and 95% confidence intervals (±CI) also given (means with different letters indicate significant different vegetation types using post hoc tests).

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[3] https://www.longpaddock.qld.gov.au/silo

of these sandplain shrublands experienced more than one fire in this period (**Table 1**), although very few areas were burnt three or more times (<1% of this vegetation type). Although sandplains dominate the study area, especially the southern portion, accounting for about 42% of the total area, fires preferentially occur here as they account for about 84% of the total burned area (**Table 1**).

Fires were less common in other vegetation types (**Table 1**) and were rare in saltmarsh and mulga vegetation, mainly occurring where such vegetation bordered sandplain shrublands (**Figure 1**). Fires burning in sandplain shrublands also occasionally crossed into and burnt the edges of neighboring eucalypt woodland on alluvial drainage lines and plains. However, in the very south of the study area, some fires burn right through these eucalypt woodlands patches (**Figure 1**). Although some 20% of the eucalypt woodlands has experienced fire in the last 50 years, almost none of these burnt areas have experienced repeated fire (**Table 1**).

Individual fires also showed a clear preference for sandplain shrublands burning significantly more than expected based on available area, whereas fires clearly avoided saltmarsh, eucalypt woodlands and mulga vegetation, burning well below what was available (**Table 1**). Individual fires in shrublands on greenstone/ironstone uplands tended to burn areas equivalent to their availability (**Table 1**).

Fire Re-occurrence and Patterns Within Vegetation Types

For most of the vegetation types studied, the bulk of their area remained unburnt over the ∼58 years of fire records, with very few areas experiencing more than one fire (**Table 1**). The clear exception was the sandplain shrublands where roughly 45% by area had experienced one fire and ∼20% two fires (**Table 1**). The major wildfires (by extent) in these shrublands could be grouped into two discrete 2–3 year periods (1966–1969, and 2000–2002; **Figure 2**). Around 66% of sandplain areas burnt in these large fires of late 1960s were burnt again in early 2000s (**Table 2**) and indeed fires in 2000–2002 were much more likely to occur in areas burnt in the 1966–1969 fires than areas not burnt by these fires relative to the area available (**Table 2**).

Of the major vegetation types, it was only in sandplain shrublands where fires were more likely to occur distant from its edge (i.e., boundary with other vegetation types) than close to its edge. Eucalypt woodland was more likely to burn in areas close to its edge, whereas for all other types no preference in terms of position of fires relative to their edges was found (**Table 3**).

Temporal Fire Patterns and Fire Intervals

Except for the aforementioned two periods 1967–1969 and 2000–2002 when several large wildfires occurred (e.g., four fires each exceeding 100 km^2 occurred in December 2000, January 2001, February 2002 and December 2002), most years experienced either no fires or only relatively small fires in terms of burn area (**Figure 2**). Annual burn area was positively correlated with regional rainfall experienced in the second year prior to the fire year (r = 0.35), as well as 2–3 years of cumulative rainfall in years preceding the fire (i.e., not including year of fire; **Table 4**), whereas the (3-year) cumulative burn area was positively correlated with rainfall in the second and third years prior to fire (r = 0.36 and 0.39, respectively) and cumulative rainfall totals spanning from 2 to 4 years prior (**Table 4**). The strongest correlation found was between cumulative 3-year burn area and cumulative 3 years of rainfall in years prior to fire year (r = 0.52). Eucalypt woodland burn area was more strongly correlated with regional rainfall in the 2 years prior to fire year (r = 0.44) than was burn area in sandplain shrublands (r = 0.36; **Table 4**).

TABLE 2 | Comparison of two periods experiencing very large wildfires in the study area (1966–1969 and 2000–2002) showing areas (and percentage) of total sandplain shrubland burnt and unburnt in 1966–1969 and the area (and percentage) of these burnt in later fires of 2000–2002.

	Total area available		**Area burnt 2000–2002**		**Selection**
	km^2	**%**	**km^2**	**%**	**Ratio**
Burnt 1966–1969	374.3	24.2	245.7	38.4	1.59
Unburnt 1966–1969	1,173.7	75.8	393.5	61.6	0.81
Total	1,548.0	100	639.2	100	–

Selection ratio is the proportion burnt in 2000–2002 relative to area available.

The time-series analyses (SEA) showed that years with major fire events were more likely to occur when the second year prior to fire year had significantly higher than average rainfall, as well when there were sequences of years with above average rainfall prior to the year of fire (**Table 4**). However, there were no significant deviations between average rainfall and rainfall in years with fire (of all sizes), nor in years with no fire (**Table 4**).

Fire interval estimation using survival analysis was only possible for the two most common vegetation types. In terms of the fitted Weibull model, parameter b was ∼124 for sandplain shrublands, which can be interpreted as the estimated fire interval (in years) that will be exceeded ∼37% of the time. This translates into an estimated median fire interval of 103 years for this vegetation type (**Table 5**). The estimated parameter c of 1.95 indicates an almost linear increase in fire hazard over time. In contrast, the estimated median fire interval for eucalypt woodlands was much longer (870 years although with relatively large standard error), and the parameter c estimate of 1.25 suggests closer to constant fire hazard over time (which is indicated by a value of 1; Moritz et al., 2004).

DISCUSSION

Landscape Fire Preferences

Our spatial analyses of fires across the landscape show wildfires clearly favor shrublands on yellow sandplains over other vegetation, with both individual fires and overall burn area preferencing this widespread vegetation type. Fires in these shrublands are typically large intense crown fires because, given sufficient time since fire, the vegetation develops dense and reasonably continuous canopies over large areas (Braun, 2006; Dalgleish et al., 2015; Kelso et al., 2015). Within these shrublands,

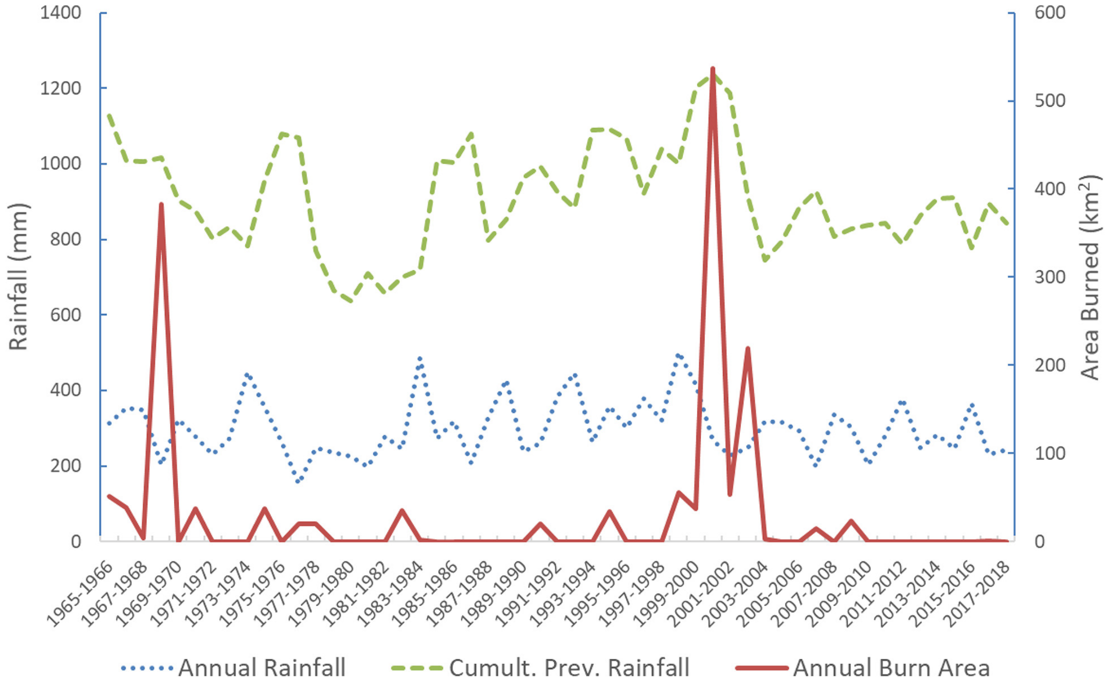

FIGURE 2 | Relationships between annual rainfall, previous 3-year rainfall and burn area (all based on financial year). Both regional average rainfall for each financial year and cumulative 3-year rainfall (total rainfall from 1 to 3 years prior to financial year) are shown.

TABLE 3 | Mean distance (m) of 1,000 randomly selected points to the nearest edge of its vegetation type for burnt and unburnt points.

Veg/land type	Mean distance from edge of vegetation type (s.e.)		*df*	*t*	*p*
	Unburnt (1960–2018)	Burnt (1960–2018)			
Acacia sandplain shrubland	585 (41)	798 (33)	511	−4.02	<0.001
Eucalypt woodland on alluvium	412 (20)	283 (31)	288	2.75	0.009
Mulga plains and hardpans	359 (39)	150 (83)	38	1.48	0.074
Salt lakes and fringing saltmarsh	442 (49)	399 (15)	40	0.93	0.85
Shrublands on greenstone-ironstone hills	415 (42)	430 (66)	79	−0.69	0.95
All types	442 (6)	656 (9)	972	−8.10	<0.001

fires tended to be non-random, preferentially burning away from edges and in areas burnt by previous large fires, suggesting some ecological memory in terms of fire pathways (Peterson, 2002; Johnstone et al., 2016). Preference for reburning of previously burnt vegetation has been reported in a range of vegetation types, and generally reflects either positive feedbacks where fires increase the flammability of vegetation, or that fire pathways are shaped by inherent landscape patterns of vegetation, topography and/or ignition sources (Pausas et al., 2017; McLauchlan et al., 2020). In a nearby region, O'Donnell et al. (2011b) found connectivity of more flammable vegetation across the landscape was critical in determining fire spread and, therefore, fire intervals, which seems to be important in our study area as well given many areas of the long-unburnt sandplain shrubland occurred in isolated patches surrounded by less flammable vegetation types, such as salt lakes/pans and woodlands (**Figure 1**). Preferential burning manifests itself in the uneven spatial distribution and configuration of long-unburnt patches of sandplain shrublands across our study landscape, which will be the subject of a future paper given such patches have been demonstrated to be vital habitat for certain species of birds (Davis et al., 2016), reptiles and small mammals (Doherty et al., 2015), and plants (Knuckey et al., 2016).

Other shrubland types occur in the study area but these are generally less dense and occupy relatively small and isolated areas (e.g., ironstone hills, greenstone ranges), and so experience relatively few fires (which are mostly started by lightning or by people who use existing roads and tracks network which tend to be away from uplands; Braun, 2006). Saltmarsh shrublands also experienced few fires, which is expected given the generally low flammability of the sparse and mostly succulent vegetation (van Etten and Burrows, 2018).

TABLE 4 | Fire–rainfall relationships shown for single year and multi-year (cumulative) totals using (1) correlations between annual burn areas and annual rainfall (upper half of table); and (2) anomalies between mean annual rainfall associated with fire event year(s) and long-term regional averages (1968–2018) expressed as standard scores (lower half).

Fire parameter	Annual rainfall (relative to year of fire occurrence)								
	t_0	t_{-1}	t_{-2}	t_{-3}	$t_{-1\ to\ 0}$	$t_{-2\ to\ 0}$	$t_{-3\ to\ 0}$	$t_{-2\ to\ -1}$	$t_{-3\ to\ -1}$
Annual burn area	−0.14	0.20	0.35*	0.15	0.035	0.22	0.27	0.37**	0.37**
3 year burn area	0.02	0.21	0.36*	0.39*	0.14	0.31	0.46**	0.38**	0.52***
Sandplain shrubland annual burn area	−0.17	0.19	0.35*	0.17	0.023	0.21	0.26	0.36**	0.38**
Eucalypt woodland annual burn area	−0.074	0.23	0.37**	0.085	0.11	0.29*	0.30*	0.44**	0.37**
Fire years	0.013	0.15	0.21	0.38	0.11	0.20	0.36	0.24	0.40
Non-fire years	−0.008	−0.09	−0.13	−0.24	−0.07	−0.13	−0.23	−0.15	−0.25
Major fire years	0.090	0.40	0.92*	0.65	0.33	0.77	0.99*	0.96*	1.16*

Year of rainfall and fire based on financial year (i.e., July 1–June 30 of following year) in line with main fire season. For both analyses, year of fire event is t_0, t_{-1} is year before fire event, t_{-2} is 2 years before fire, and so on. For cumulative totals across several preceding years: $t_{-1\ to\ 0}$ refers to total rainfall over fire year and previous year, $t_{-2\ to\ 0}$ for total rainfall from fire year to 2 years previous, etc. Asterisks show significant correlations or significant deviations from long-term mean rainfall ($p < 0.05$; **$p < 0.01$; ***$p < 0.001$).*

TABLE 5 | Parameters of Weibull model fitted to fire interval data for two major vegetation types of study area.

Vegetation type	Parameter	Estimate	Std error	Z	P
Sandplain	Intercept	4.819	0.0832	57.9	<<0.001
Shrublands	Log (scale)	−0.665	0.078	−8.91	<<0.001
	Scale	0.514	0.041		
	b	123.88	3.51		
	c	1.95	0.16		
	MEI	102.9 yrs	4.45		
Eucalypt	Intercept	7.061	0.837	8.18	<<0.001
Woodland	Log (scale)	−0.226	0.109	−2.06	0.0391
	Scale	0.798	0.087		
	b	1,165.71	395.3		
	c	1.25	0.14		
	MEI	870.1 yrs	322.5		

MEI refers to median Weibell fire interval in years; b and c are standard Weibull curve parameters.

The second-most burnt vegetation type was eucalypt woodland (with 17% of its area burnt at least once) but, in contrast to sandplain shrublands, fires here occurred mostly near the edges, entering from adjoining vegetation types. This vegetation is sensitive to fire, with the dominant eucalypt trees tending to be killed outright when burnt, although seedling regeneration has been reported to be strong following fire, as is typical of obligate seeders (Hollenbach, 2008; Gosper et al., 2013a, 2016). Fire is rare in the other type of woodland of the study area, the mulga woodlands in the northern part of study area, which agrees with what is known for this vegetation type across arid Australia (Murphy et al., 2013; van Etten and Burrows, 2018).

Fire Intervals

Average (median) fire return intervals were estimated to be around 100 years in sandplain shrublands with fire hazard and likelihood increasing linearly with time since last fire, although well-above rainfall periods were also found to contribute to the likelihood of large fires in this vegetation. This average interval aligns with known fuel dynamics for these shrublands with total fuel loads accumulating slowly and gradually after fire for at least 50–80 years with little evidence of plateau or peaks in fuel loads over this timeframe (Dalgleish et al., 2015). Fuel accumulation is so slow and patchy across these shrublands that it is unlikely that extensive wildfires can occur again for at least 20 years, and up to 30 years, post fire, which aligns with the general paucity of areas burnt twice across our ∼50 year study period (representing only 20% of shrubland area) and almost no areas burnt three times. Most of twice-burnt areas were located in the largest continuous swathes of sandplain shrublands in the southern part of the study area, with most of these being areas burnt by major wildfires in mid-late 1960s and again by large wildfires between 2000 and 2002 (representing a 32–36 year interval). These decadal-scale fire intervals are similar to that reported for sandplain shrublands in the Lake Johnston area, some 400 km to the south-east, although within the same broad rainfall zone (O'Donnell et al., 2011b). Studies of other semi-arid shrublands have also reported linearly increasing fire hazard with time (McCaw, 1997; O'Donnell et al., 2011b; Fernandes et al., 2012), although shrublands in other generally wetter and more coastal Mediterranean-type climates, both in Australia and elsewhere, generally seem to have a weaker relationship between vegetation age and fire hazard, with fire weather seemingly more important (Moritz et al., 2004; Van Wilgen et al., 2010; Fontaine et al., 2012).

The eucalypt woodlands, in contrast, have typically very long fire intervals (estimated at 870 years on average, although highly variable) with only minor increases in fire hazard over time and a slightly stronger link between above-average rainfall and fire occurrence. This concords with other studies of valley-floor eucalypt woodlands in the broader "transitional-rainfall" region of Western Australia in terms of their very long fire intervals, low fuel levels and accumulation rates, and the importance of large rainfall events in promoting fires (O'Donnell et al., 2011b; Gosper et al., 2013a,b), characteristics which Gosper et al. (2016) argue separate them from other eucalypt woodland ecosystems of Australia, such as savanna and temperate grassy woodlands.

Fire Drivers

Large deluges of rain, or sustained periods of above-average rainfall, are likely to temporally increase fuel levels and connectivity in the eucalypt woodlands through promotion of annual plants, particularly grasses (O'Donnell et al., 2011a), which is a common driver of fire occurrence in many arid ecosystems (Balch et al., 2013; Gibson et al., 2015; van Etten and Burrows, 2018). Importantly, fire was most closely associated with rain 2 years before fire, which suggests that a period of drying and curing of annual plants is required before fuels become flammable. This explains fire traveling through large patches of eucalypt woodland around 1–3 years following the period May 1998–April 2000 during which over twice the usual rainfall occurred in the study area, which corresponds to one of the wettest periods in inland southern Western Australia for 200 years (O'Donnell et al., 2018). In most other circumstances, fire only traveled into these woodlands (from shrublands) for a short distance at their edge, which could reflect transitional fuel configurations and/or fire weather conditions at edges (Gartner et al., 2012; Driscoll et al., 2021). More research is needed to quantify fuel levels of eucalypt woodlands, both at edges and in the interior, and especially following wet periods, to confirm that rainfall is a major driver of fires via temporary fuel enhancement. Further, many eucalypt woodlands in the study area were grazed by sheep until about 2003, which may have played a role in suppressing fuel levels up to this time.

Fire occurrence in sandplain shrublands was also positively associated with rainfall before fire events, although correlations were more modest. These shrublands lack grasses, and their high density/cover tends to discourage ground annuals, so wet episodes may stimulate shrub growth and continuity, thereby promoting fire. This finding, however, is at odds with that reported for many other dense shrubland ecosystems where drought has been reported to promote crown fires through lowering fuel moisture and increasing the dead fuel component (Keeley et al., 2012; Turco et al., 2017). Ladbrook et al. (2018) found positive associations between pre-fire rainfall and fire extent in more open *Acacia* shrublands in arid Western Australia (some 500 km north-west of our study area) with most burning occurring in the years after an extremely wet period in that region. Indeed, across Australia's arid zone, fire activity is strongly linked to antecedent rainfall (Turner et al., 2008), as we report here. It may be that major wet-dry cycles are critical in promoting fires, as has been reported in some arid ecosystems (Balch et al., 2013), and more analysis is recommended to explore relationships between fire and climatic fluctuations. Although we found a negative correlation between fire extent and rainfall in the fire year, it was not statistically significant. Further, the role of fire weather (temperature, humidity and wind speed during and in days preceding the fire) in driving fire spread needs further exploration given its importance in other shrubland ecosystems (Keeley et al., 2012; Clarke et al., 2014; Keeley and Syphard, 2019); unfortunately such pre-fire weather data was absent for the vast majority of our mapped fire scars.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Studies of fire regimes and their drivers typically seek generalizations based on climate or region (e.g., Rodrigues et al., 2019). Much of our study landscape is dominated by a complex mosaic of two distinct vegetation types which were found to have highly contrasting fire regimes—one a dense shrubland prone to intense crown fires at relatively modest intervals, although with strongly developed adaptations to regenerate after fire (via both seedlings and resprouting; Knuckey et al., 2016); the other a low-fuel woodland ecosystem dominated by a fire-sensitive obligate seeder, where fires are very rare and limited mostly to edges. Such divergent fire regimes and preferential burning patterns have been reported across many other arid and semi-arid landscapes in Australia (Nicholas et al., 2011; van Etten and Burrows, 2018) and elsewhere (Heyerdahl et al., 2001; McLauchlan et al., 2020).

Fire drivers operating in each of our two major vegetation types also appear to be different in some respects, albeit both show a clear positive response to pre-fire rainfall. In the shrubland, fire age is important in shaping fire hazard, albeit over decadal scales. However, the role of rainfall in driving fire occurrence and hazard is more clear-cut in woodlands as fuels tend to remain low and patchy, and do not accumulate except following ample rainfall. These woodlands, therefore, subscribe to the fuel-limited model of fire regimes characteristic of arid lands (Pausas and Ribeiro, 2013). Drivers of shrubland fires in our study area, on the other hand, are only fuel limited during recovery following wildfire (which is relatively slow), but not when mature. However, there is no strong evidence that fire in mature shrubland is drought-driven as is the case with shrubland ecosystems from more productive (mesic) climates (Pausas and Ribeiro, 2013).

Woodland and shrublands ecosystems are often adjoining each other in our study area so the critical ecological question is how do the such disparate fire regimes develop and persist in proximity? Fundamentally, the vegetation patterning across the landscape is an expression of the mosaic of different soil and landform types (specifically sandplain and alluvial drainage systems for these two main vegetation types, respectively). The ecotone between these two vegetation types is of particular interest as this is where vegetation properties will intergrade and where fire is most likely to cross-over from shrubland and enter woodland ecosystems (Gartner et al., 2012). Ecotones between fire-prone and fire sensitive vegetation can be dynamic, changing with fire history, and can be challenging to manage (Nicholas et al., 2011; Just et al., 2016). However, they also provide opportunities to protect fire sensitive vegetation through active fuel management or clearing of fire breaks located near edges (Parks et al., 2015). Management should aim to limit or constrain large summer wildfires in sandplain shrublands, especially as they can burn into fire sensitive woodland and other vegetation types, and also reduce the extent of long unburnt shrubland habitat that is so vital for certain species of flora and fauna in our study area.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

EE, TD, and RD wrote and edited the manuscript. EE analyzed the data. All authors contributed to the article and approved the submitted version.

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REFERENCES

Allan, G. E., and Southgate, R. I. (2002). “Fire regimes in the spinifex landscapes of Australia,” in *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*, eds R. A. Bradstock, J. E. Williams, and A. M. Gill (Cambridge: Cambridge University Press), 145–176.

Archibald, S., Roy, D. P., van Wilgen, B. W., and Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biol.* 15, 613–630. doi: 10.1111/j.1365-2486.2008.01754.x

Avitabile, S. C., Callister, K. E., Kelly, L. T., Haslem, A., Fraser, L., Nimmo, D. G., et al. (2013). Systematic fire mapping is critical for fire ecology, planning and management: case study in the semi-arid Murray Mallee, south-eastern Australia. *Landscape Urban Plan.* 117, 81–91. doi: 10.1016/j.landurbplan.2013.04.017

Balch, J. K., Bradley, B. A., D’Antonio, C. M., and Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biol.* 19, 173–183. doi: 10.1111/gcb.12046

Beard, J. S., Beeston, G. R., Harvey, J. M., Hopkins, A. J. M., and Shepherd, D. P. (2013). *The Vegetation of Western Australia at the 1: 3,000,000 Scale. Explanatory Memoir*, 2nd Edn, Vol. 9. Perth, WA: Conservation Science Western Australia, 1–152.

Boschetti, L., Roy, D. P., Giglio, L., Huang, H., Zubkova, M., and Humber, M. L. (2019). Global validation of the collection 6 MODIS burned area product. *Remote Sens. Environ.* 235:111490. doi: 10.1016/j.rse.2019.111490

Bowman, D. M., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., et al. (2009). Fire in the Earth system. *Science* 324, 481–484. doi: 10.1126/science.1163886

Braun, K. (2006). *Fire Management Charles Darwin Reserve*. Melbourne: Australian Bush Heritage Fund.

Burrows, N. D., and Christensen, P. E. S. (1990). “A survey of Aboriginal fire patterns in the Western Desert of Australia,” in *Fire and the Environment: Ecological and Cultural Perspectives, Proceedings of an International Symposium, Knoxville, Tennessee*, eds S. C. Nodvin and A. W. Thomas (Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station), 297–305.

Callister, K. E., Griffioen, P. A., Avitabile, S. C., Haslem, A., Kelly, L. T., Kenny, S. A., et al. (2016). Historical maps from modern images: using remote sensing to model and map century-long vegetation change in a fire-prone region. *PLoS One* 11:e0150808. doi: 10.1371/journal.pone.0150808

Chree, C. (1913). Some phenomena of sunspots and of terrestrial magnetism at Kew Observatory. *Philos. T. Roy. Soc. A* 212, 75–116.

Clarke, P. J., Knox, K. J., Bradstock, R. A., Munoz-Robles, C., and Kumar, L. (2014). Vegetation, terrain and fire history shape the impact of extreme weather on fire severity and ecosystem response. *J. Veg. Sci.* 25, 1033–1044. doi: 10.1111/jvs.12166

Dalgleish, S. A., van Etten, E. J. B., Stock, W. D., and Knuckey, C. (2015). Fuel dynamics and vegetation recovery after fire in a semiarid Australian shrubland. *Int. J. Wildland Fire* 24, 613–623. doi: 10.1071/WF14128

Davis, R. A., Doherty, T. S., van Etten, E. J., Radford, J. Q., Holmes, F., Knuckey, C., et al. (2016). Conserving long unburnt vegetation is important for bird species, guilds and diversity. *Biodivers. Conserv.* 25, 2709–2722. doi: 10.1007/s10531-016-1196-5

Diex, D. M. (2013). *Survival Analysis in R*. Available online at: https://www.openintro.org/download.php?file=survival_analysis_in_R&referrer=/stat/surv.php (accessed March 15, 2020).

Doherty, T. S., Davis, R. A., van Etten, E. J. B., Collier, N., and Krawiec, J. (2015). Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire. *Int. J. Wildland Fire* 24, 534–543. doi: 10.1071/WF14115

Doherty, T. S., van Etten, E. J. B., Davis, R. A., Knuckey, C., Radford, J. Q., and Dalgleish, S. A. (2017). Ecosystem responses to fire: identifying cross-taxa contrasts and complementarities to inform management strategies. *Ecosystems* 20, 872–884. doi: 10.1007/s10021-016-0082-z

Driscoll, D. A., Armenteras, D., Bennett, A., Brotons, L., Clarke, M., Doherty, T. S., et al. (2021). How fire interacts with habitat loss and fragmentation. *Biol. Rev.* 96, 976–988. doi: 10.1111/brv.12687

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., et al. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biol. Conserv.* 143, 1928–1939. doi: 10.1016/j.biocon.2010.05.026

ESRI (2011). *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.

Fernandes, P. M., Loureiro, C., Magalhães, M., Ferreira, P., and Fernandes, M. (2012). Fuel age, weather and burn probability in Portugal. *Int. J. Wildland Fire* 21, 380–384. doi: 10.1071/WF10063

Fontaine, J. A., Westcott, V. C., Enright, N. J., Lade, J. C., and Miller, B. P. (2012). Fire behaviour in south-western Australian shrublands: evaluating the influence of fuel age and fire weather. *Int. J. Wildland Fire* 21, 385–395. doi: 10.1071/WF11065

Gartner, M. H., Veblen, T. T., Sherriff, R. L., and Schoennagel, T. L. (2012). Proximity to grasslands influences fire frequency and sensitivity to climate variability in ponderosa pine forests of the Colorado Front Range. *Int. J. Wildland Fire* 21, 562–571. doi: 10.1071/WF10103

Gibson, R. K., Bradstock, R. A., Penman, T., Keith, D. A., and Driscoll, D. A. (2015). Climatic, vegetation and edaphic influences on the probability of fire across mediterranean woodlands of south—eastern Australia. *J. Biogeogr.* 42, 1750–1760. doi: 10.1111/jbi.12547

Gosper, C. R., Prober, S. M., and Yates, C. J. (2013a). Multi-century changes in vegetation structure and fuel availability in fire-sensitive eucalypt woodlands. *Forest Ecol. Manag.* 310, 102–109. doi: 10.1016/j.foreco.2013.08.005

Gosper, C. R., Prober, S. M., and Yates, C. J. (2016). Continental—scale syntheses of Australian pyromes – misclassification of south—western eucalypt woodlands misinforms management. *J. Biogeogr.* 43, 858–861. doi: 10.1111/jbi.12693

Gosper, C. R., Prober, S. M., Yates, C. J., and Wiehl, G. (2013b). Estimating the time since fire of long-unburnt *Eucalyptus salubris* (Myrtaceae) stands in the Great Western Woodlands. *Aust. J. Bot.* 61, 11–21. doi: 10.1071/BT12212

He, T., Lamont, B. B., and Pausas, J. G. (2019). Fire as a key driver of Earth’s biodiversity. *Biol. Rev.* 94, 1983–2010. doi: 10.1111/brv.12544

Heyerdahl, E. K., Brubaker, L. B., and Agee, J. K. (2001). Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. *Ecology* 82, 660–678.

Hollenbach, M. B. (2008). *Fire Ecology and Management of Eucalyptus loxophleba Woodlands in the Northern Wheatbelt of Western Australia*. diploma thesis.

Hanover: Institute of Geobotany & Institute of Environmental Planning, Leibniz University of Hannover.

Hopper, S. D., and Gioia, P. (2004). The southwest Australian floristic region: evolution and conservation of a global biodiversity hotspot. *Annu. Rev. Ecol. Syst.* 35, 623–650. doi: 10.1146/annurev.ecolsys.35.112202.130201

Johnson, E. A., and Gutsell, S. L. (1994). "Fire frequency models, methods and interpretations," in *Advances in Ecological Research*, Vol. 25, eds M. Begon and A. H. Fitter (London: Academic Press), 239–287.

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., et al. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14:369–378. doi: 10.1002/fee.1311

Just, M. G., Hohmann, M. G., and Hoffmann, W. A. (2016). Where fire stops: vegetation structure and microclimate influence fire spread along an ecotonal gradient. *Plant Ecol.* 217, 631–644. doi: 10.1007/s11258-015-0545-x

Kane, V. R., Lutz, J. A., Cansler, C. A., Povak, N. A., Churchill, D. J., Smith, D. F., et al. (2015). Water balance and topography predict fire and forest structure patterns. *Forest Ecol. Manag.* 338, 1–13. doi: 10.1016/j.foreco.2014.10.038

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., and Rundel, P. W. (2012). *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge: Cambridge University Press.

Keeley, J. E., and Syphard, A. D. (2019). Twenty-first century California, USA, wildfires: fuel-dominated vs. wind-dominated fires. *Fire Ecol.* 15, 24. doi: 10.1186/s42408-019-0041-0

Kelso, J. K., Mellor, D., Murphy, M. E., and Milne, G. J. (2015). Techniques for evaluating wildfire simulators via the simulation of historical fires using the Australis simulator. *Int. J. Wildland Fire* 24, 784–797. doi: 10.1071/WF14047

Knuckey, C. G., van Etten, E. J., and Doherty, T. S. (2016). Effects of long−term fire exclusion and frequent fire on plant community composition: a case study from semi−arid shrublands. *Aust. Ecol.* 41, 964–975. doi: 10.1111/aec.12388

Ladbrook, M., van Etten, E. J. B., and Stock, W. D. (2018). Contemporary fire regimes of the arid Carnarvon Basin region of Western Australia. *Fire* 1:51. doi: 10.3390/fire1030051

Manly, B., McDonald, L. L., and Thomas, D. L. (1993). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. London: Chapman and Hall.

McCarthy, M. A., Gill, A. M., and Bradstock, R. (2001). Theoretical fire-interval distributions. *Int. J. Wildland Fire* 10, 73–77. doi: 10.1071/WF01013

McCaw, W. L. (1997). *Predicting Fire Spread in Western Australian Mallee-Heath Shrubland*. Ph.D thesis. Canberra: University College, University of New South Wales.

McKenzie, D., and Littell, J. S. (2017). Climate change and the eco−hydrology of fire: will area burned increase in a warming western USA? *Ecol. Appl.* 27, 26–36. doi: 10.1002/eap.1420

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., et al. (2020). Fire as a fundamental ecological process: research advances and frontiers. *J. Ecol.* 108, 2047–2069. doi: 10.1111/1365-2745.13403

Moreira, F., Vaz, P., Catry, F., and Silva, J. S. (2009). Regional variations in wildfire susceptibility of land-cover types in Portugal: implications for landscape management to minimize fire hazard. *Int. J. Wildland Fire* 18, 563–574. doi: 10.1071/WF07098

Moritz, M. A., Keeley, J. E., Johnson, E. A., and Schaffner, A. A. (2004). Testing a basic assumption of shrubland fire management: how important is fuel age? *Front. Ecol. Environ.* 2:67–72.

Murphy, B. P., Bradstock, R. A., Boer, M. M., Carter, J., Cary, G. J., Cochrane, M. A., et al. (2013). Fire regimes of Australia: a pyrogeographic model system. *J. Biogeogr.* 40, 1048–1058. doi: 10.1111/jbi.12065

Nicholas, A. M. M., Franklin, D. C., and Bowman, D. M. J. S. (2011). Floristic uniformity across abrupt boundaries between *Triodia* hummock grassland and *Acacia* shrubland on an Australian desert sandplain. *J. Arid Environ.* 75, 1090–1096. doi: 10.1016/j.jaridenv.2011.06.016

O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2011b). Vegetation and landscape connectivity control wildfire intervals in unmanaged semi−arid shrublands and woodlands in Australia. *J. Biogeogr.* 38, 112–124. doi: 10.1111/j.1365-2699.2010.02381.x

O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2011a). Climatic anomalies drive wildfire occurrence and extent in semi−arid shrublands and woodlands of southwest Australia. *Ecosphere* 2, 1–15. doi: 10.1890/ES11-00189.1

O'Donnell, A. J., Cook, E. R., Palmer, J. G., Turney, C. S., and Grierson, P. F. (2018). Potential for tree rings to reveal spatial patterns of past drought variability across western Australia. *Environ. Res. Lett.* 13:024020. doi: 10.1088/1748-9326/aaa204

Oliveira, S., Moreira, F., Boca, R., San-Miguel-Ayanz, J., and Pereira, J. M. (2014). Assessment of fire selectivity in relation to land cover and topography: a comparison between Southern European countries. *Int. J. Wildland Fire* 23, 620–630. doi: 10.1071/WF12053

Parks, S. A., Holsinger, L. M., Miller, C., and Nelson, C. R. (2015). Wildland fire as a self−regulating mechanism: the role of previous burns and weather in limiting fire progression. *Ecol. Appl.* 25, 1478–1492. doi: 10.1890/14-1430.1

Parsons, B. C., and Gosper, C. R. (2011). Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. *Int. J. Wildland Fire* 20, 184–194. doi: 10.1071/WF09099

Pausas, J. G., and Bradstock, R. A. (2007). Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. *Global Ecol. Biogeogr.* 16, 330–340. doi: 10.1111/j.1466-8238.2006.00283.x

Pausas, J. G., Keeley, J. E., and Schwilk, D. W. (2017). Flammability as an ecological and evolutionary driver. *J. Ecol.* 105, 289–297. doi: 10.1111/1365-2745.12691

Pausas, J. G., and Paula, S. (2012). Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. *Global Ecol. Biogeogr.* 21, 1074–1082. doi: 10.1111/j.1466-8238.2012.00769.x

Pausas, J. G., and Ribeiro, E. (2013). The global fire–productivity relationship. *Global Ecol. Biogeogr.* 22, 728–736. doi: 10.1111/geb.12043

Payne, A. L., Van Vreeswyk, A. M. E., Leighton, K. A., Pringle, H. J., and Hennig, P. (1998). *An Inventory and Condition Survey of the Sandstone-Yalgoo-Paynes Find area, Western Australia. Technical Bulletin No. 90*. Western Australia: Department of Agriculture and Food.

Peterson, G. D. (2002). Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5, 329–338. doi: 10.1007/s10021-001-0077-1

Rodrigues, M., Costafreda-Aumedes, S., Comas, C., and Vega-García, C. (2019). Spatial stratification of wildfire drivers towards enhanced definition of large-fire regime zoning and fire seasons. *Sci. Total Environ.* 689, 634–644. doi: 10.1016/j.scitotenv.2019.06.467

Rogeau, M. P., Flannigan, M. D., Hawkes, B. C., Parisien, M. A., and Arthur, R. (2016). Spatial and temporal variations of fire regimes in the Canadian Rocky Mountains and Foothills of southern Alberta. *Int. J. Wildland Fire* 25, 1117–1130. doi: 10.1071/WF15120

Schoennagel, T., Smithwick, E. A., and Turner, M. G. (2009). Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA. *Int. J. Wildland Fire* 17, 742–753. doi: 10.1071/WF07146

Sherriff, R. L., and Veblen, T. T. (2008). Variability in fire–climate relationships in ponderosa pine forests in the Colorado Front Range. *Int. J. Wildland Fire* 17, 50–59. doi: 10.1071/WF07029

Shu, S., Metcalfe, G., Müller, C., and Cann, P. (2004). "Application of remote sensing in fire management in Western Australia," in *Proceedings of the Australasian Fire Authorities Annual Conference, 7-9 October 2004*, Perth, WA.

Turco, M., von Hardenberg, J., AghaKouchak, A., Llasat, M. C., Provenzale, A., and Trigo, R. M. (2017). On the key role of droughts in the dynamics of summer fires in Mediterranean Europe. *Sci. Rep.* 7:81. doi: 10.1038/s41598-017-00116-9

Turner, D., Ostendorf, B., and Lewis, M. (2008). An introduction to patterns of fire in arid and semi-arid Australia, 1998-2004. *Rangeland J.* 30, 95–107. doi: 10.1071/RJ07039

Turner, M. G., Hargrove, W. W., Gardner, R. H., and Romme, W. H. (1994). Effects of fire on landscape heterogeneity in Yellowstone National Park. Wyoming. *J. Veg. Sci.* 5, 731–742. doi: 10.2307/3235886

Turner, M. G., and Romme, W. H. (1994). Landscape dynamics in crown fire ecosystems. *Landscape Ecol.* 9, 59–77. doi: 10.1007/BF00135079 van Etten, E. J. B., and Burrows, N. D. (2018). "Fire regimes and ecology of arid Australia," in *On the Ecology of Australia's Arid Zone*, ed. H. Lambers (Dordrecht: Springer), 243–282. doi: 10.1007/978-3-319-93943-8_10

Van Wilgen, B. W., Forsyth, G. G., de Klerk, H., Das, S., Khuluse, S., and Schmitz, P. (2010). Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *J. Appl. Ecol.* 47, 631–638. doi: 10.1111/j.1365-2664.2010.01800.x

Xu, T., and Hutchinson, M. (2011). *ANUCLIM Version 6.1 User Guide. Canberra: Fenner School of Environment and Society*. Canberra: The Australian National University.

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Rainfall-Linked Megafires as Innate Fire Regime Elements in Arid Australian Spinifex (*Triodia* spp.) Grasslands

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Large, high-severity wildfires, or “megafires,” occur periodically in arid Australian spinifex (*Triodia* spp.) grasslands after high rainfall periods that trigger fuel accumulation. Proponents of the patch-burn mosaic (PBM) hypothesis suggest that these fires are unprecedented in the modern era and were formerly constrained by Aboriginal patch burning that kept landscape fuel levels low. This assumption deserves scrutiny, as evidence from fire-prone systems globally indicates that weather factors are the primary determinant behind megafire incidence, and that fuel management does not mitigate such fires during periods of climatic extreme. We reviewed explorer’s diaries, anthropologist’s reports, and remotely sensed data from the Australian Western Desert for evidence of large rainfall-linked fires during the pre-contact period when traditional Aboriginal patch burning was still being practiced. We used only observations that contained empiric estimates of fire sizes. Concurrently, we employed remote rainfall data and the Oceanic Niño Index to relate fire size to likely seasonal conditions at the time the observations were made. Numerous records were found of small fires during periods of average and below-average rainfall conditions, but no evidence of large-scale fires during these times. By contrast, there was strong evidence of large-scale wildfires during a high-rainfall period in the early 1870s, some of which are estimated to have burnt areas up to 700,000 ha. Our literature review also identified several Western Desert Aboriginal mythologies that refer to large-scale conflagrations. As oral traditions sometimes corroborate historic events, these myths may add further evidence that large fires are an inherent feature of spinifex grassland fire regimes. Overall, the results suggest that, contrary to predictions of the PBM hypothesis, traditional Aboriginal burning did not modulate spinifex fire size during periods of extreme-high arid zone rainfall. The mechanism behind this is that plant assemblages in seral spinifex vegetation comprise highly flammable non-spinifex tussock grasses that rapidly accumulate high fuel loads under favorable precipitation conditions. Our finding that fuel management does not prevent megafires under extreme conditions in arid Australia has parallels with the primacy of climatic factors as drivers of megafires in the forests of temperate Australia.

Keywords: arid vegetation, fire ecology, grass-fire feedbacks, patch-burning, indigenous land management

INTRODUCTION

Large-scale high-intensity conflagrations occur during periods of meteorological extreme in many fire-prone ecosystems (Keeley and Fotheringham, 2001; Gill and Allan, 2008; Bradstock, 2010). Proponents of the patch-burn mosaic (PBM) hypothesis propose that such fires are anomalous in the modern era and are primarily the result of (1) the cessation of indigenous "patch-burning" practices that previously kept landscape-level fuel loads low; and (2) European fire-suppression practices that protect grazing lands and infrastructure but also promote widespread fuel accumulation (Bonnicksen, 1981; Minnich, 1983; Goforth and Minnich, 2007). A key assumption of the PBM hypothesis is that fuel age has a positive association with ecosystem flammability (Moritz et al., 2004; Goforth and Minnich, 2007). Accordingly, under the PBM hypothesis, when landscapes are broken up into mosaics of early and late successional vegetation, large high-intensity wildfires should be rare due to the inability of early seral vegetation to carry fire (Minnich, 1983, 1998).

Despite being an attractive hypothesis that has underpinned fire management activities in many fire-prone regions, the universal applicability of the PBM hypothesis is now being questioned (Gill, 2000; Moritz et al., 2004; Keeley and Zedler, 2009; Kimber and Friedel, 2015). Fire researchers in North America have demonstrated that for many American ecosystems, the assumed relationship between post-fire successional state and flammability does not hold (Keeley and Fotheringham, 2001; Moritz et al., 2009). For example, in ponderosa pine (*Pinus ponderosa* Douglas ex. C. Lawson) forests and chaparral shrublands, early seral states are characterized by fine surface layer fuels composed of highly flammable grasses and shrubs. Modeling has shown that these fuels carry fire well, even under relatively low wind situations, and are unlikely to act to as fire-retardant breaks under any fire weather (Moritz et al., 2004; Keeley and Zedler, 2009). In these systems, fire occurrence is driven more by extremes of meteorological variables such as temperature, humidity, and wind speed, rather than time-since-fire and associated characteristics of the fuel array (Keeley and Fotheringham, 2001).

A widespread Australian ecosystem for which the applicability of the PBM hypothesis has also been questioned are the spinifex (*Triodia* R. Br.) grasslands of arid and semiarid Australia (Gill, 2000; Kimber and Friedel, 2015; **Figures 1A–D**). Contemporary fire cycles in these grasslands are characterized by periodic wildfires that are large in scale (e.g., occasionally exceeding 10,000 km^2) (Allan and Southgate, 2002), high in intensity (e.g., up to c. 14,000 kW; Burrows et al., 1991), and driven by fuel accumulations that occur following exceptionally high rainfall years (Griffin et al., 1983; Allan and Southgate, 2002). A long-held assumption about fire in these grasslands is that large fires during the pre-European period were rare and were constrained by traditional Aboriginal burning that maintained fuel load heterogeneity in landscapes (Jones, 1969; Gamage, 2012). Evidence that supports this hypothesis comes from studies of aerial photos that clearly show small fire patch sizes under traditional burning regimes (Burrows and Christensen, 1990; Burrows and Chapman, 2018) and from satellite-image-derived fire scar analyses indicating that contemporary Aboriginal burning buffers climate-driven increases in fire size (Bliege Bird et al., 2012).

There is little doubt that in many regions, prior to European contact, skilled and purposeful burning by Aboriginal peoples maintained landscape mosaics comprised of fire scars of different post-fire ages. These fires were crucial for human survival in spinifex grasslands, as a means of increasing hunting capture rates and promoting the growth of food plants (O'Connell et al., 1983; Bird et al., 2008; Latz, 2018). Nevertheless, several lines of evidence suggest that big spinifex grassland fires did occur during the pre-contact period:

1. Anecdotal reports from formerly "traditional-living" Aboriginal peoples of large fires occurring when traditional patch burning was being practiced. These reports come from the spinifex-dominated Gibson and Great Sandy Deserts and include mention of fires that would "go for five nights" or that could be followed for "up to a few days" and of very large wildfires that "finish 'im up everything, right up …." (Mutitjulu community and Baker, 1996; Yates and Morse, 2003; Burrows et al., 2006a). Such fires are reported to have forced people to abandon large areas for a time, as game and plant foods became scarce as burnt regions recovered (Yates and Morse, 2003).
2. Contemporary observations of large fires in recently burnt spinifex grassland subject to high post-fire rainfall (i.e., two large fires with an inter-fire interval of c. 2–3 years) (Latz, 1990, 2007; Gill, 2000; Allan and Southgate, 2002; Allan et al., 2003; Matthews, 2005; Wright, 2007; Wright and Clarke, 2007; Duguid et al., 2008). These observations reflect that post-fire seral state spinifex, which is usually dominated by highly flammable non-spinifex tussock grasses such as *Aristida holathera* Domin. (**Figure 1C**), can accumulate fuels quickly under high rain conditions and burn as readily, albeit at lower

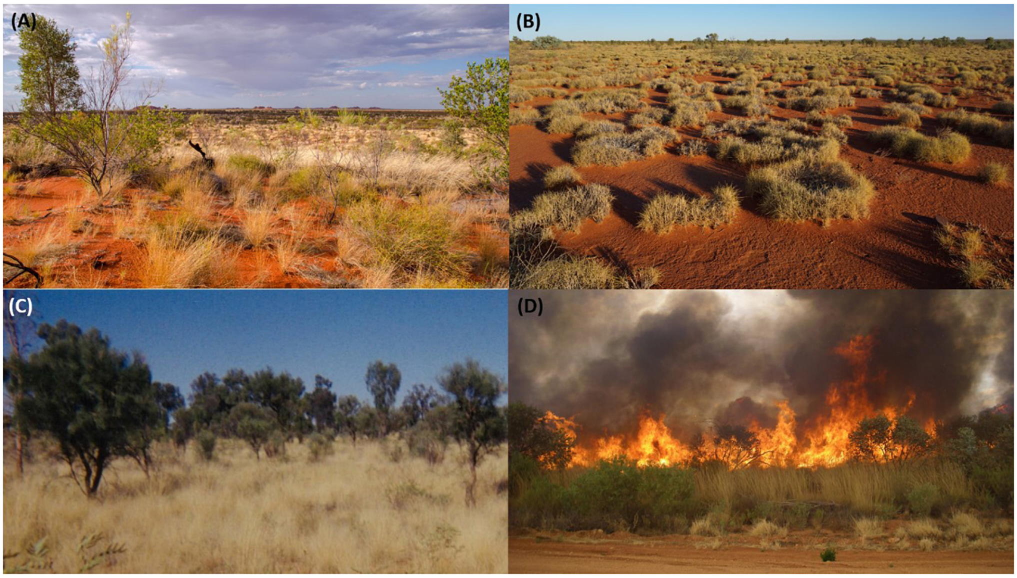


FIGURE 1 | (A) Regenerating *Triodia epactia* grassland in central Gibson Desert during average rainfall conditions in 2015. **(B)** Long-unburnt *Triodia basedowii*-dominated grassland in eastern Gibson Desert during average rainfall conditions in 2017. **(C)** Early post-fire seral spinifex vegetation in Haasts Bluff Aboriginal Land Trust in far-eastern Western Desert during well-above average rainfall conditions in 2002. *Aristida holathera* is the main ground layer biomass component. **(D)** Lightning-ignited fire in *Triodia pungens*-dominated grassland on Deep Well station, central Australia. This fire occurred in November 2012 when widespread spinifex fuel accumulations occurred following exceptionally high rainfall years in 2010–2011. *Triodia* flowering culms double the height of the ground fuel layer.

intensity, as old growth spinifex (see **Table 1** for list of common seral spinifex species).

3. Incursions of large spinifex wildfires into central Australian conservation reserves where patch-burn fire management has been practiced. In these reserves, good rainfall seasons in 1983–1984, 2000–2002, and 2010–2011 led to massive fuel accumulations and subsequent wildfires that either burnt over the top of previously instated patch mosaics or trickled around the patch burns and burnt large areas (Allan and Baker, 1990; Allan et al., 2003; Duguid et al., 2008; Horn and Liston, 2013).

Given the broad-scale nature of prescribed management burning in Australian spinifex grassland reserves, further assessment of the efficacy of patch burning to constrain large-scale wildfires during periods of climatic extreme is warranted. Here, we examined the records of arid Australian explorers, anthropologist's reports, and remotely sensed data for evidence of a "rainfall–fire size" relationship in spinifex grasslands during the pre-contact period when traditional Aboriginal burning was being practiced. We restricted our search to the Western Desert, as the vegetation of this region is primarily spinifex grassland and several expeditions passed through it when traditional Aboriginal patch burning was still occurring. To ascertain the likely seasonal conditions associated with each of the expeditions, we examined (1) El Niño Southern Oscillation (ENSO) patterns derived from Oceanic Niño Index (ONI) data and (2) precipitation records from the late 1860s to present from long-term weather stations located on the periphery of the arid zone in southern South Australia (Orroroo), southwestern NSW (Wentworth), and central QLD (Springsure). ENSO conditions are usually associated with continental-scale fluctuations in rainfall variability and are known to be primary drivers of interannual variability of fire weather (Harris and Lucas, 2019). Rainfall data from the various weather stations, although spatially distant from the Western Desert, were also considered useful,

TABLE 1 | Common seral spinifex species by % composition by weight and time-since-fire for maximum biomass levels according to Latz (1990) and TERN (2019).

Species	Family	Reported % composition of post-fire seral vegetation by weight (range)	Time (post-fire) for maximum biomass
Chrysocephalum apiculatum	Asteraceae	10	Uncertain
Crotalaria eremea	Fabaceae	25	1
Senna pleurocarpa	Fabaceae	20–50	2–4
Tephrosia sphaerospora	Fabaceae	50	1
Scaevola parviflora	Goodeniaceae	35	1
Aristida holathera	Poaceae	20–80	1–4
Aristida inaequiglumis	Poaceae	8–12	2
Eragrostis eriopoda	Poaceae	3–35	2–7
Eriachne helmsii	Poaceae	13	2
Eulalia aurea	Poaceae	15	Unclear
Panicum decompositum	Poaceae	5	1
Paraneurachne muelleri	Poaceae	10–35	1–5
Yakirra australiense	Poaceae	10	0.5

as extreme-high-rainfall activity in the Australian arid and semiarid zones is often experienced at the continental scale (Denniston et al., 2015).

During our literature search, we encountered several Western Desert mythologies that mention large-scale wildfires. As indigenous oral traditions can sometimes corroborate historic events (Nunn and Reid, 2015), we provide a very brief description of these fire myths in our "Results" section and outline the massive scale of the fires that are mentioned. Additionally, as a final exercise, we conducted a satellite imagery study from a spinifex-dominated region in the southwest of the Northern Territory where large areas (c. 500,000 ha) were reported of have burnt twice in 2 years in the early 1980s following successive years of high rainfall (Allan and Southgate, 2002). Doing this exercise would demonstrate unequivocally whether recently burnt patches of spinifex grassland can re-burn rapidly if high post-fire rainfalls occur. This, by corollary, would provide an examination of the tenet of the PBM hypotheses that a relationship exists between fuel age and flammability in the spinifex system.

MATERIALS AND METHODS

Study Area—The Western Desert

The study area was the Western Desert, a large arid plateau occurring primarily in the Western Australian interior and extending into the far northwest of South Australia and the southwest corner of the Northern Territory. It covers an area of approximately 800,000 km^2 and encompasses the Gibson, the Great Victoria, the Great Sandy, and the Little Sandy Deserts. Geographically, the Desert is composed primarily of large sections of arid dunefield and sandplain interspersed with occasional salt lakes, clay pans, and mountain ranges. Climatically, its summers are hot, with mean maximum temperatures during the hottest month (January) reaching the mid-high 30s. Winters are cool, with mean maximum temperatures in the coolest month (July) rarely rising above 20°C. Typical of other arid Australian regions, rainfall is unpredictable, with some years receiving little or (rarely) no precipitation and others experiencing monsoon-linked deluges. Annual average rainfall ranges from 180 mm in the southeast of the Desert (Cook BOM station, SA) to 360 mm in the northwest (Telfer Aero BOM weather station) (Australian Government Bureau of Meteorology, 2021).

Study Community—Arid Spinifex Grasslands

Triodia is a large genus of perennial hummock-forming grasses that dominate grassland and savannah-type systems over approximately 26.6% of the Australian continent (AUSLIG, 1990). As aridity generally limits fuel quantity and fuel continuity in these systems, large fires usually only occur after sufficient rainfall has occurred to promote lateral expansion of hummocks and growth of interstitial species (Allan and Southgate, 2002; Armstrong, 2011). Spinifex species themselves are coarse, occasionally resinous, and sometimes form rings as plants age and die out in the center. Tall flowering culms are highly flammable when dry and can raise the fuel heights of plants to 1.5 m (Jessop, 1981). Fuel loads in long-unburnt grassland range from 1.6 to >12 tons ha^{-1}, depending on fuel age and whether the fuel array consists purely of *Triodia* spp. or includes woody species (Winkworth, 1967; Beadle, 1981; Burrows et al., 2006b).

The vegetation of recently burnt spinifex grassland is quite different to that of long-unburnt grassland. In regions dominated by obligate-seeding *Triodia*, fire kills adult plants, and post-fire rainfall triggers the proliferation of spinifex seedlings, non-spinifex grasses, forbs, and shrub and tree seedlings (**Table 1**; Latz, 1990; Wright and Clarke, 2007; TERN, 2019). This successional pattern reflects release from competition after adult spinifex death, with smaller-statured non-spinifex species taking advantage of increased light, nutrient, and water availability in the post-fire environment (Griffin, 1990). Non-spinifex species usually make up the bulk of early post-fire fuels in seeder-dominated grassland, with maximum biomass of these species generally peaking within 2–3 years post-fire. Spinifex seedlings may also contribute to the early post-fire fuel array (up to 50% of the fuel biomass under certain circumstances; Latz, 1990). However, the proportion of post-fire fuels comprised by spinifex seedlings is variable and depends on several factors, including (1) post-fire rainfall season and volume; (2) the species of spinifex involved; and (3) whether mature *Triodia* populations had masted recently prior to fire (masting "tops up" seed banks and maximizes seed availability for post-fire spinifex seedling recruitment) (Wright and Fensham, 2018). In spinifex grasslands dominated by resprouting *Triodia*, early post-fire successional states are generally dominated by vegetatively regenerating spinifex hummocks rather than by short-lived non-spinifex grasses and forbs (Latz, 1990).

Estimating Fire Sizes

We located numerous explorer's observations that allowed empiric estimation of pre-contact fire sizes in the Western Desert (**Table 2** and **Figure 2**). Where possible, the approximate localities of the fires were identified. We followed the method used by Gill (2000) to produce a "conservative" estimate and a "less-conservative" estimate of fire size based on estimates of distances traveled over burnt ground. Conservative fire size estimates were calculated by taking the length of traverse over burnt country as the length of an elliptical fire with a length:breadth ratio of 2:1. The rationale for the use of ellipses here was that, in linear dunefield environments such as those in the Western Desert, fires frequently burn within dune valleys and are often stopped by high dune crests that act as fire breaks. This, in combination with windy conditions, often results in burn scars that are elliptical in shape. For each fire, a "less conservative" estimate of fire size was made by taking the reported length of traverse over burnt country as the diameter of a circular fire.

As part of our review of pre-contact Western Desert fires, we examined fire scars on Landsat satellite imagery taken during the 1970s in the Lake Mackay region of Western Australia. In this region, the last group of never-before-contacted Aboriginal people (referred to in contemporary media as the "Pintupi Nine") had been conducting traditional burning and living a hunter-gatherer lifestyle until 1984 (Guilliatt, 2010). In the mid-1970s,

TABLE 2 | Summary of observations of pre-contact fire sizes in Western Desert.

	Region	Observation	Estimated fire size (assuming circular fires)	Seasonal conditions	References
1873	Northern Great Victoria Desert	27 miles of burnt ground traveled over 2 days	c. 148,000 ha	Favorable	Warburton, 1875
1873	Gibson Desert	"Many miles of burnt, stony, gravelly undulations; at every four or five miles I obtained a view of similar country beyond . . ."	Not clear, could be up to c. 45,000 ha fire if obtained a "similar view" of burnt country on at least three occasions (i.e., 3 × 4–5 miles)	Favorable	Giles, 1889a
1874	Gibson Desert	Spinifex fires that "run on for scores of miles" (i.e., 40, 60 or more miles)	c. 731,000 ha (if fires ran on for 60 miles)	Favorable	Giles, 1889b
1874	Great Victoria Desert	"Four miles north were then traveled, over burnt country, ..."	c. 3,250 ha	Favorable	Giles, 1889b
1889	Eastern Gibson Desert	". . . 3 or four miles these had been swept by fire, . . ."; ". . . five miles distant; all the country in that direction seems to have been recently burnt."	c. 1,800–5,077 ha	Average	Tietkens, 1890
1936	Eastern Gibson Desert	A horseshoe shaped fire, 2 miles long, one mile wide.	c. 500 ha	Below average	Finlayson (1936) in Gill, 2000
1953	Gibson Desert	NA (satellite imagery)	<10–1,744 ha	Average	Burrows and Christensen, 1990
1960/1961	Great Victoria Desert	NA (satellite imagery)	<1–3593 ha	Average	Burrows and Chapman, 2018
c. 1960	Warburton, Northern Great Victoria Desert	(Referring to hunting fires) ". . . many hundreds of meters wide and extending for some kilometers."	10–3,000 ha	Average	De Graaf (1975) in Gill, 2000
c. 1960	Great Sandy Desert	Empiric description of hunting fire patch sizes given	800–2,500 ha	Average	Gould (1980) in Gill, 2000

Method for estimating fire size based on Gill (2000).

one of the largest rainfall systems in history passed over northern Australia (Denniston et al., 2015; **Figure 2** and online appendices 1, 2). We were interested to examine whether there was evidence of a shift in fire scar patterning in the region where the Pintupi Nine people had been burning before and after this high-rainfall period occurred. For this study, we examined imagery from 1972, a time of average to slightly above-average rainfall, and from 1979, which was when the next imagery was available after the mid-1970s rains. We mapped the fire scars for this study using Landsat 1 and 3 satellite images (WRS paths 113 and 114 and WRS rows 75 and 76; i.e., four scenes in total for each of the two time periods), and the satellite data were accessed from the USGS Earth Explorer (available at https://earthexplorer.usgs.gov/). The scenes were displayed with bands 3, 4, and 2 as red, green, and blue, respectively, to enhance the discrimination of fire scars. The 1979 scars were mapped in ArcGIS manually by drawing polygons around fire scars from a difference image created using imagery from 1972 and 1979. All scars on the 1972 image were mapped since no difference image could be created, as there was no previous Landsat image. The extent of the fires went well beyond the four chosen Landsat scenes. However, we limited the mapping to the extent of the four mentioned scenes.

For the early 1980s "short-interval fire mapping" study, we used Landsat 4 and 5 imagery (WRS paths 104 and 105 and rows 76 and 77) downloaded from the USGS Earth Explorer (available at https://earthexplorer.usgs.gov/). Scenes from 1982 were compared with those from 1983 (an interval of about 6 months) to create a difference image. The scars of the fires were digitized in ArcGIS. The same methodology was repeated for the fires over the summer of 1984–1985. The fire scars of interest were all completely contained within the examined Landsat scenes.

RESULTS

Pre-contact Fire

Several observations were made by explorers that indicate that large fires were occurring during the pre-contact period in the Western Desert. These observations were made in the early-mid 1870s during expeditions led by Col. P. Egerton-Warburton (hereafter referred to as Col. Warburton) and W.E.P. (Ernest) Giles (**Table 2** and **Figure 2**). From the long-term weather data, seasonal conditions during these expeditions appear to have been highly favorable. The ONI for 1870 was −1.0 or lower across all weather stations, suggesting that La Niña conditions prevailed

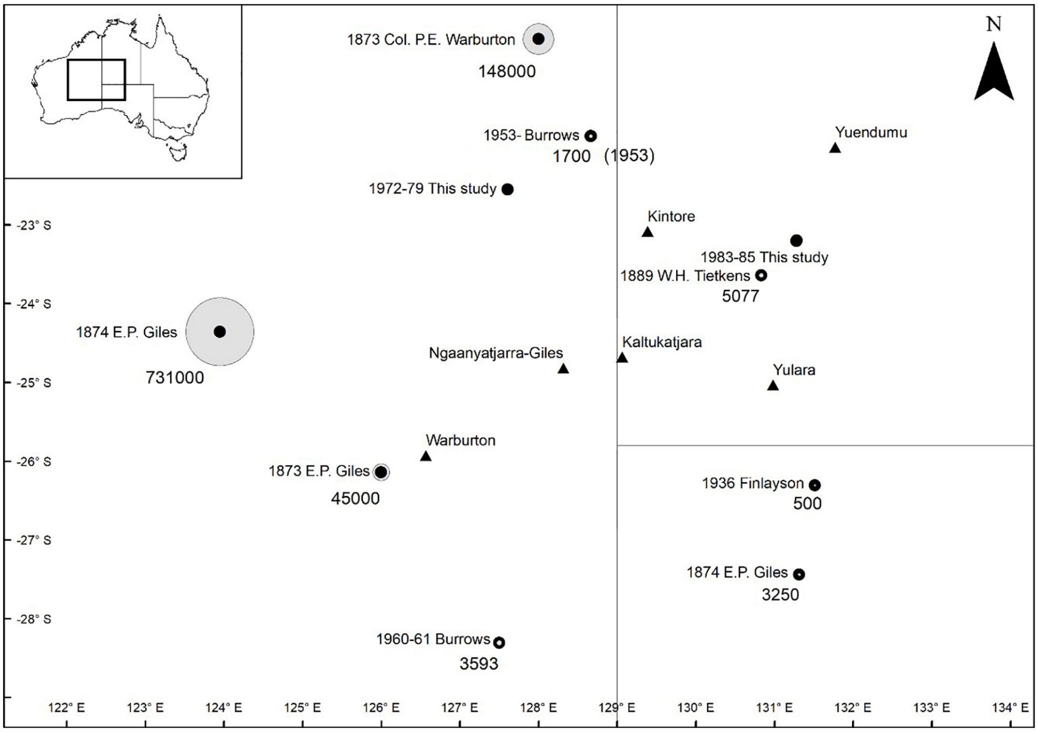


FIGURE 2 | Map showing approximate locations of explorer's observations of pre-contact fires in Western Desert. Circle size corresponds to relative fire sizes. Numbers associated with circles indicate estimated fire sizes (ha). Where observations give a range of fire sizes, the larger fire size is presented. Gray lines indicate Australian state and territory boundaries (South Australia, Western Australia, and Northern Territory). Triangles indicate large contemporary settlements and weather stations.

and that higher-than-average rainfall would have occurred across much of northern and central Australia during the summer of 1870/1871 (**Figure 3**). Rainfall records of Springsure, Wentworth, and Ororroo weather stations provide further evidence that a continental-scale extreme wet period had occurred at this time (**Figure 3** and **Supplementary Appendix Figures 1**, **2**). All stations showed extreme-high-rainfall years in the early 1870s, with 1870 being the highest rainfall year on record for the Wentworth and Orroroo weather stations and the fifth highest rainfall year on record for Springsure (Australian Government Bureau of Meteorology, 2021).

Both Giles and Col. Warburton mentioned large-scale fires during their expeditions. While traveling through the Mt Wilson region of Western Australia in 1873, Col. Warburton traveled over 27 miles (43.5 km) of burnt ground over 2 days. This suggests a minimum fire size of c. 58,000 ha (assuming an elliptical fire with a 2:1 length:breadth ratio) and a maximum fire size of c. 148,000 ha (assuming a circular fire). Giles, while traveling through the southern Gibson Desert in 1876, estimated that under high-wind conditions, fires in spinifex habitat could "run on for scores of miles," implying that he had observed fires that had burnt for distances of at least 40 miles (64 km) but possibly up to 60 miles (96 km) or more. If the fires he had witnessed had been 40 miles in cross section, then burnt areas could have been between 163,000 (assuming elliptical fires) and 325,000 ha (assuming fires were circular). If the fires had run for three score miles (96 km), then areas burnt could have been between 366,000 ha (if elliptical fires) and 731,000 ha (if circular fires).

There were several observations of smaller fires (<1 to c. 5000 ha) during unexceptional rainfall years in the late nineteenth and early- to mid-twentieth centuries. These include observations made by Tietkins, Finlayson, Burrows and Christenson, De Graaf, and Gould (**Table 2** and **Figure 2**). From our remote sensing study of the Lake Mackay region, numerous smaller fires were observed on the 1972 imagery, which may have been, at least partially, the result of traditional burning conducted by the Pintupi Nine (**Figure 4**). These small-scale fires were obliterated in the 1979 imagery, which showed c. 7.17 million ha (i.e., 66%) of the mapped area burnt. These large-scale fires presumably occurred in response to fuel accumulations after the record-breaking rains of 1974/1975. It could be argued that these 1970s fire observations are irrelevant to the PBM hypothesis, as low population size would have limited the spatial extent of patch burning by the Pintupi Nine. By this time, other traditional-living Aboriginal peoples in the region had come out of the desert and were settled in communities such as Haasts Bluff, Papunya, and Balgo (Hansen, 1984; Heffernan, 1984). However, population densities in the extreme-low productivity Gibson Desert were always low, traditionally in the order of 1 person per 200 - 260 km^2 (Long, 1971), so the images may still be relevant.

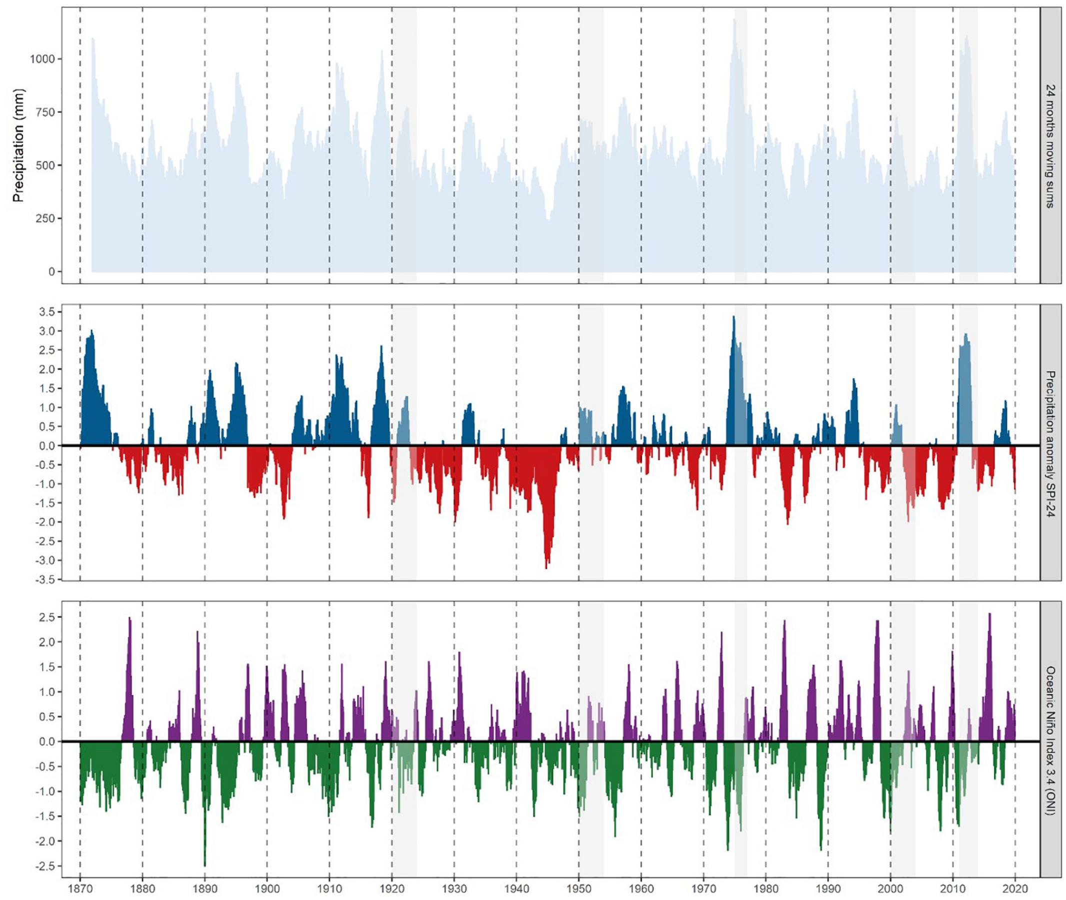


FIGURE 3 | Twenty-four-month cumulative rainfall and rainfall anomaly data from Wentworth weather station in southwest NSW. Bottom panel shows Oceanic Niño Index (ONI) 3.4 from 1870 to present. Major rainfall events/periods associated with big arid zone wildfires are shown in gray bands.

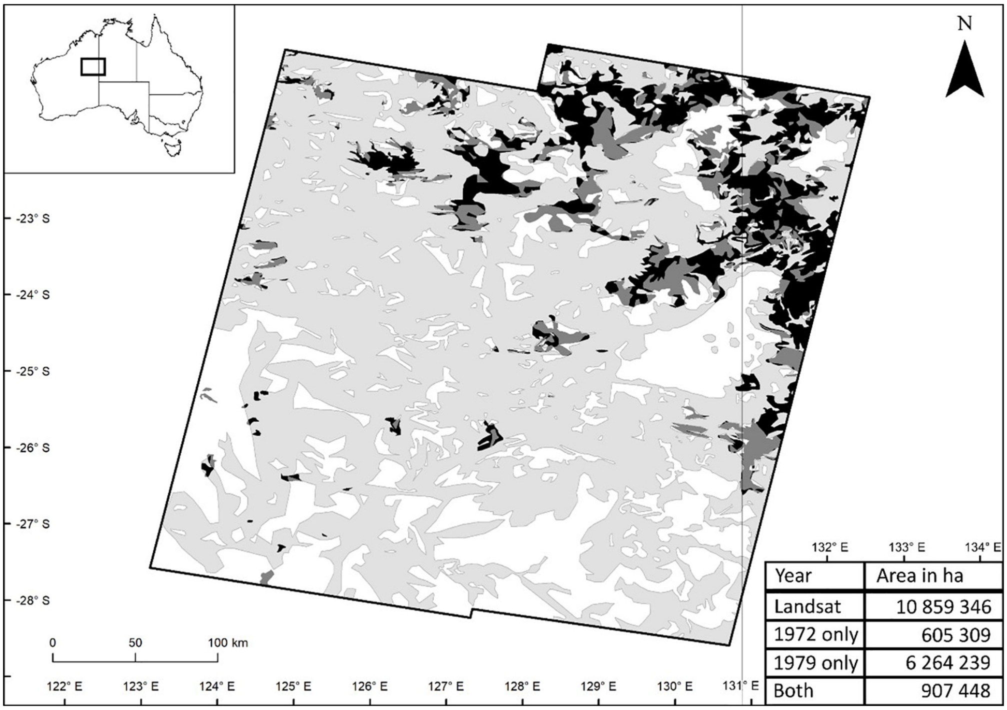
Aboriginal Fire Myths

Several Western Desert myths were identified that mentioned extreme-large scale fires. In the Warlukurlangu myth (Kimber, 1983), a large blaze ignited by the lungkata (blue tongue) ancestral spirit began in Warlpiri tribal country close to present-day Yuendumu community and burnt in a southward direction to Pitjantjatjara country, some 400-km distant. The minimum dimensions of this fire, if circular, would have been c. 12.6 million ha, and if an ellipse with a 2:1 length:breadth ratio, would have been c. 6.3 million ha. In another myth, from the arid Lake Mackay region of Western Australia, a large fire that ignited close to the edge of Lake Mackay forced an ancestral being to flee underground to Nyinmi rock hole, some 150 km to the southwest (Tjupurrula, 2014). If this fire had burnt all the way to Nyinmi, then the approximate dimensions of this fire would have been c. 1.8 million ha if circular and c. 0.9 million ha if an ellipse with a 2:1 length:breadth ratio.

There are also several mythologies from arid regions outside the Western Desert that report large spinifex fires. These include the "Ahiite" myth, where a large fire begins in Alyawarra country on the Sandover River and burns across 350 km in a southwest direction to Rubuntja, a fire dreaming site of the Aranda tribe in the western MacDonnell ranges (Moyle and Morton, 1986; Memmott, 1992). There is also an Alyawarra "traveling fire dreaming," which concerns a fire that begins near the Plenty river in the southern Northern territory and burns across c. 400 km of the *Triodia* dominated Wakaya Desert to the Table Top region in western Queensland, c. 40 km southwest of Camooweal (Keys and Memmott, 2016; Memmott, P. pers. Comm. 2021).

1980s Short-Interval Fires

Our mapping of the 1980s short interval fires from the southwest Northern Territory confirmed the report of Allan and Southgate (2002) that large areas of spinifex grassland had re-burnt in this region only 2 years after initial fires had occurred. The mapping showed that fires in late 1982/early 1983 burnt c. 1.95 million ha. These fires presumably occurred in response to rainfall-triggered fuel accumulations after exceptionally high rains in 1981–1982 (**Figure 5**). During this time, the Derwent meteorological station in the far NE of study area indicates 932-mm rainfall fell in the 18-m period prior to April 1982 (the Derwent has an annual average precipitation of 327 mm) (**Supplementary Appendix Figure 4**; Australian Government Bureau of Meteorology, 2021). Approximately



Year	Area in ha
Landsat	10 859 346
1972 only	605 309
1979 only	6 264 239
Both	907 448

FIGURE 4 | 1970s fire scars from homelands of the Pintupi Nine, west of Lake Mackay in the Gibson Desert, Western Australia. Fires in light gray were evident on 1979 satellite imagery and are presumed to have occurred in response to fuel accumulations after high rainfall years of 1974/1975. Fires in black were burnt twice (1972 and 1979), and areas in dark gray were burnt in 1972 only. White areas were unburnt throughout study period.

2 years later, large fires in late 1984 burnt c. 1 million ha in the region, with c. 470,000 ha burning over areas that had already burnt in 1982/1983. These follow-up fires presumably occurred in response to fuel accumulations triggered by continued exceptionally high rainfall in 1983 and early 1984 (**Figure 5** and **Supplementary Appendix 3**). During this time, the Derwent rainfall records indicate that 719-mm rainfall fell during the 18-month period prior to April 1984 (**Supplementary Appendix Figure 4**; Australian Government Bureau of Meteorology, 2021).

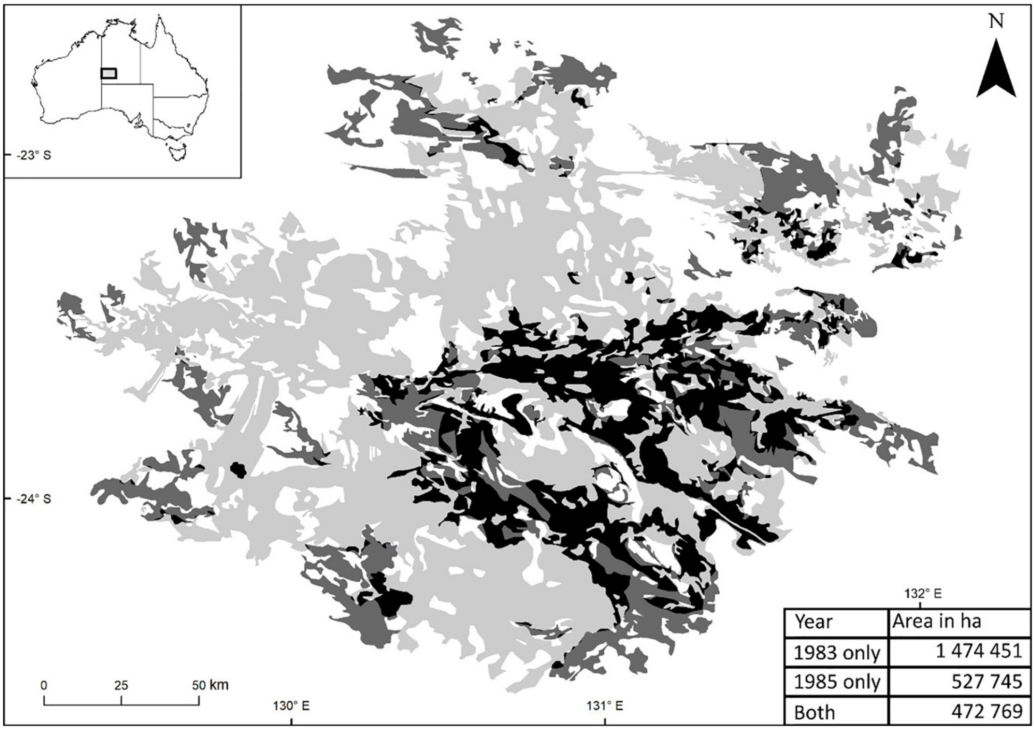
DISCUSSION

Pre-contact Fire Sizes

The fires identified by Col. Warburton in 1873, Giles in 1873 and 1874, and the 1970s Lake Mackay mapping of this study are examples of massive rainfall-linked fires during the pre-European period when traditional Aboriginal patch burning was still being practiced. The size of these fires is similar in scale to larger arid Australian wildfires recorded following high-rainfall periods in the contemporary era (Griffin et al., 1983; Allan and Southgate, 2002; Allan et al., 2003; Verhoeven et al., 2020) and dwarfs modern fires observed during periods of average or below-average rainfall (Turner et al., 2008). Observations of large pre-contact fires directly contradict one of the central tenets of the PBM hypothesis—that indigenous patch burning should constrain large wildfires by fragmenting landscapes and breaking up fuel loads (Minnich, 1983, 1998). They are, however, consistent with paleoecological (dendrochronological) records from the United States that indicate episodic large-scale fires were a prominent feature in certain American pre-contact landscapes, despite frequent burning by indigenous people (Mensing et al., 1999).

Additional evidence that large-scale spinifex fires occurred during the pre-European period may come from Western Desert Aboriginal fire mythologies. Previous authors have suggested that indigenous oral traditions can corroborate real events from the temporally distant past (i.e., euhemerism) (Vitaliano, 1973; Barber and Barber, 2004). Nunn and Reid (2015) have argued that because Australian Aboriginal cultural protocols place great importance on traditional knowledge, precise transgenerational transmission of oral traditions can occur over exceptionally long time periods. Extremely large wildfires in several Western Desert Aboriginal mythologies could therefore derive from real fires from the ancient pre-contact period. The scale of the fires mentioned in the myths is massive and, if they were actual fires, would have left large tracts of country uninhabitable for a period and presumably left long-lasting impressions on Aboriginal peoples living in the burnt regions.

A highly referenced series of pre-contact Aboriginal fire scars from the Western Desert are those captured by the 1953 Blue Streak and 1960/1961 aerial photography (Burrows and Chapman, 2018; Clark, 2020). These fire observations have been held as strong evidence that the pre-contact fire



Year	Area in ha
1983 only	1 474 451
1985 only	527 745
Both	472 769

FIGURE 5 | Large-scale short-interval wildfires in west central Australia in the early 1980s. Patches in light gray show the extent of a single fire that occurred in 1982/1983. Patches that are dark gray burnt in 1984/1985 and patches that are black burnt in both periods. White areas within the 1982/1983 fire were unburnt throughout the study period. Rainfall during the study period at "The Derwent" weather station is given in **Supplementary Appendix 4**.

regime of the Western Desert was characterized by patchy, small-scale, cool-season fires and that large summer fires in the contemporary era are anomalous. However, to properly determine if traditional burning constrained large rainfall-linked fires would require assessing imagery taken at a time of known high rainfall when widespread fuel accumulations would have been present. Although some parts of Australia were very wet in the early 1950s, especially western Queensland (see Springsure data—**Supplementary Appendix Figure 2**), weather records are available for the early 1950s from the Giles Metrological and Warburton weather stations. Both stations are within c. 150 km of the areas captured in the Blue Streak and 1960/1961 aerial photography, and both indicate only average to slightly below-average rainfall conditions during the years immediately prior to the time the photos were taken (Australian Government Bureau of Meteorology, 2021; **Supplementary Appendix 4**).

Short-Interval Spinifex Fires

Our mapping of large, short-interval fires during a high-rainfall period in the Western Desert in the 1980s demonstrates unequivocally that the effectiveness of recently burnt areas to act as fire breaks can degenerate rapidly when rainfall conditions are good. Such observations of rainfall-triggered short-interval (2–3 years) fires in spinifex grasslands are not unique, with numerous other studies/authors having reported short-interval spinifex grassland fires on Aboriginal lands (Allan and Southgate, 2002; Wright, 2007), pastoral properties (Latz, 1990; Allan and Southgate, 2002), and fire-managed arid conservation reserves such as Uluru Kata-Tjuta (Ayer's Rock) National Park (Allan et al., 2003) and Finke Gorge National Park (Matthews, 2005).

The mechanism that allows post-fire seral spinifex to return to a flammable state quickly after high rainfall is rapid growth rates of highly flammable non-spinifex grass and forb species (Latz, 1990; Allan and Southgate, 2002). The C_4 tussock grass, kerosene grass (*Aristida holathera*), is one of the most important contributors by weight in seral spinifex vegetation, comprising up to 80% of vegetation biomass in the first 2 years after fire (**Figure 1C** and **Table 1**; Griffin et al., 1983; Latz, 1990; TERN, 2019). This grass species has seeds that are triggered to germinate by smoke (Wright, 2007; Wright and Clarke, 2009), and although generally an annual, it can behave as a perennial following successive good rainfall seasons that permit continued growth (Latz, 1990). Fires fueled primarily by *A. holathera* are fast burning (hence the common name "kerosene grass"), though the fuel loads of *Aristida*-fueled fires (c. 0.5 kg m^{-2}) are lower than *Triodia*-fueled fires (c. 1.55 kg m^{-2}) (Wright and Clarke, 2008) and hence generally burn at a lower intensity.

The Evolutionary Fire Regime of Arid Spinifex Grasslands

An obvious corollary to the suggestion that large rainfall-linked spinifex grassland fires occurred during the pre-European period is that such fires also occurred during the period prior to human arrival in arid Australia, some 30–40 ka years BP (Smith, 2013). If this was the case, then large rainfall-linked megafires must be considered a feature of the "evolutionary" arid spinifex fire regime, and some signal of an adaptive influence of the fire–rainfall relationship on arid zone fauna and flora might be expected. Some authors have argued that extinctions in the modern era of many small-medium sized animals are evidence that large contemporary wildfires are aberrant and that the fauna have not adapted to them (Masters, 1993). However, recent research indicates that it is an interaction between large fires and introduced predators that has led to these extinctions, with native animals unable to cope with increased predation risk under more open habitat conditions following large-scale wildfires (Letnic and Dickman, 2006).

One possibility of an adaptive trait that relates to the arid fire–rainfall relationship is the rainfall-linked mast seeding syndromes of arid *Triodia* grasses and slender mulga (*Acacia aptaneura* Maslin and J. E. Reid) shrubs (Jacobs, 1973; Davies and Kenny, 2013; Wright et al., 2014; Wright and Fensham, 2017). Contrary to popular perception, many spinifex species rarely set seed, instead producing prodigious amounts of reproductive stems/culms that hold little or no seed in most years, and only producing large crops after exceptionally high preceding rainfall (masting) (Jacobs, 1984; Rice et al., 1994; Armstrong and Legge, 2011). As seed predation prevents large quantities of spinifex seed being stored in the soil seed bank, it would be a risky strategy to produce seed annually in arid environments with highly unpredictable rainfall. Such a strategy would also preclude obligate seeders being able to survive under a regular fire regime that was not synchronized to weather patterns, such as under the proposed PBM hypothesis. In the case of arid *Triodia* and mulga, seeding "in-synch" with arid rain–fire cycles may have been selected for because it ensures high seed-bank densities during periods when fire likelihood is high. This in turn maximizes the likelihood of dense seedling recruitment in favorable post-fire environments that are low in competition and high in moisture and nutrient availability (Wright et al., 2014; Wright and Fensham, 2018).

Patch Burning in Spinifex Grassland Reserves

Although evidence presented in this paper casts doubt on the efficacy of spinifex patch burning for preventing large rainfall-linked fires, there is no doubt that small-scale managed fires are useful in spinifex conservation reserves for a variety of other reasons. Burning increases the productivity of spinifex habitat by stimulating the germination and growth of a variety of non-spinifex plant species that are useful as food for both humans and animals. Such plants include grain-producing grass species such as *Eragrostis eriopoda* Benth. and *Yakirra australiensis* Lazarides R. D. Webster and fruit-producing plants such as *Solanum centrale* J. M. Black, *Solanum cheppendalei* Symon, and *Solanum cleistogamum* Symon (O'Connell et al., 1983; Southgate and Carthew, 2007; Latz, 2018). In parts of the Gibson Desert, spinifex burning is also used by Aboriginal peoples to enhance collection rates of seeds of serotinous species with woody fruits that only release seeds after fire (e.g., *Eucalyptus pachyphylla* F. Muell.) (Nangala et al., 2019).

Patch-burning spinifex may also be useful for reducing the likelihood of large rainfall-linked wildfires entering fire-sensitive communities like *Aluta maisonneuvei* (F. Muell.) Rye and Trudgen shrublands or mulga woodlands (Gill, 2000; Wright, 2018). Patch burning for this purpose would have to occur after rainfall-triggered fuel accumulations have already occurred (to prevent patches from re-burning) and would have to be targeted around the edges of the fire-sensitive communities. The breaks would have to be burnt under low-wind/low temperature conditions to prevent fire from escaping. They would also have to be extensive in terms of spatial coverage and wide enough to prevent fire spread into the sensitive communities in the event of wildfire. Under such a management scenario, the likelihood of fire incursion into fire-sensitive vegetation should be minimized, and this should safeguard against population declines caused by repeated fires at intervals less than the *Aluta* and mulga primary juvenile periods.

A limitation of the current study is that no detail about the patchiness of pre-contact spinifex grassland megafires can be gleaned from the explorers' records. It is possible that megafires under traditional burning regimes were patchier and had greater retention of unburnt vegetation than contemporary *Triodia*-fueled wildfires. It is also possible that Aboriginal burning mitigated the ecological impacts of rainfall-linked megafires as recently burnt short grass-dominated patches would have burnt at lower intensities during megafires than mature *Triodia*-dominated vegetation. Nevertheless, as has been observed in contemporary arid zone reserves, patch burning in spinifex grasslands can lead to increased fire frequency (Allan et al., 2003; Matthews, 2005). In the absence of patch burning, arid spinifex grasslands normally only burn after high rainfall times when fuel loads are high. If patch burning takes place during average rainfall (i.e., low fuel load) years, then spinifex systems may be exposed to patch burning in these years as well as large-scale wildfires that inevitably occur following extreme-high-rainfall (i.e., high fuel load) years. At present, the state of ecological research in arid spinifex grasslands does not permit discernment of which scenario, multiple low-intensity fires, or a single high-intensity rainfall-linked megafire, is less destructive from an ecological standpoint. However, it is quite possible that the biota is resilient to a range of burning scenarios.

CONCLUSION

The PBM hypothesis was first applied in arid Australia as a means of duplicating traditional Aboriginal burning practices in desert conservation reserves (Saxon, 1984). Its implementation was intended to promote diversity in flora and fauna habitats and to constrain large-scale wildfires by reducing fuel loads. We do not dispute that pre-European burning by Aboriginal peoples was widespread and enabled human habitation in spinifex grasslands by increasing plant and animal food resources. However, evidence presented in this paper suggests that occasional large-scale wildfires are an innate feature of arid spinifex grasslands, and that PBMs can become redundant following extreme-high-rainfall periods that trigger fuel accumulation. The rainfall–fire link in arid spinifex grasslands parallels the climate–fire linkage in sclerophyll *Eucalypt*-dominated forests of temperate Australia. In these forests, periodic droughts dry out fuels and, when combined with extreme fire weather, can trigger extreme-high-intensity megafires even in regions that are fire-managed for fuel reduction (Deb et al., 2020; Ehsani et al., 2020; Bowman et al., 2021). Further research is warranted to identify other Australian vegetation types where patch-burn mosaics are unlikely to constrain megafires under extreme climatic conditions. Given the apparent inevitability of wildfires following exceptionally good seasons in arid spinifex grasslands, judicious use of scarce land management funds should focus on (1) ensuring strategic placement of infrastructure; (2) reducing anthropogenic ignitions during periods of elevated flammability; and (3) facilitation of fire-related research to assess effects of fire on the spinifex biota.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BW, RF, GA, and BL conceived and designed the research. BW conducted the literature search. DR analyzed the climate data and produced the rainfall figures. BL conducted the fire mapping. BW, GA, RF, DR, and BL wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.666241/full#supplementary-material

REFERENCES

Allan, G., and Baker, L. (1990) Uluru (Ayers Rock-Mount Olga) National Park: an assessment of a fire management program. *Pro. Ecol. Soc. Austral.* 16, 215–220.

Allan, G. E., Phillips, N. R., and Hookey, P. (2003). "Learning lessons from an exceptional period of fires in central Australia: 1999 to 2002," in *Proceedings of the 3rd International Wildland fire Conference*, Sydney, NSW.

Allan, G. E., and Southgate, R. (2002). "Fire regimes in the spinifex grasslands of Australia," in *Flammable Australia: Fire Regimes and Biodiversity of a Continent*, eds R. A. Bradstock, J. E. Williams, and A. M. Gill (Cambridge: Cambridge University Press), 145–176.

Armstrong, G. (2011). Evidence for the equal resilience of *Triodia spp*. (Poaceae), from different functional groups, to frequent fire dating back to the late Pleistocene. *Heredity* 107, 558–564. doi: 10.1038/hdy.2011.42

Armstrong, G., and Legge, S. (2011). The post-fire response of an obligate seeding *Triodia* species (Poaceae) in the fire-prone Kimberley, north-west Australia. *Int. J. Wildland Fire* 20, 974–981. doi: 10.1071/wf10130

AUSLIG (1990). *Vegetation. Atlas of Australian Resources. Third Series*, Vol. 6. Canberra, NSW: AUSLIG.

Australian Government Bureau of Meteorology (2021). *Monthly Rainfall Totals from Warburton Airfield, Giles Meteorological Station, Springsure, Wentworth, Orroroo, Cook, Telfer*. Docklands, VIC: Australian Government Bureau of Meteorology.

Barber, E. W., and Barber, P. T. (2004). *When They Severed Earth from Sky: How the Human Mind Shapes Myth*. Princeton, NJ: Princeton University Press.

Beadle, N. C. W. (1981). *The Vegetation of Australia*. Cambridge: Cambridge University Press.

Bird, R. B., Bird, D. W., Codding, B. F., Parker, C. H., and Jones, J. H. (2008). The "fire stick farming" hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proc. Natl. Acad. Sci. U.S.A.* 105, 14796–14801. doi: 10.1073/pnas.0804757105

Bliege Bird, R., Codding, B. F., Kauhanen, P. G., and Bird, D. W. (2012). Aboriginal hunting buffers climate-driven fire-size variability in Australia's spinifex grasslands. *Proc. Natl. Acad. Sci. U.S.A.* 109, 10287–10292. doi: 10.1073/pnas.1204585109

Bonnicksen, T. M. (1981). Brushland fire-management policies: a crossimpact simulation of southern California. *Environ. Manag.* 5, 521–529. doi: 10.1007/bf01866725

Bowman, D., Williamson, G. J., Price, O. F., Ndalila, M. N., and Bradstock, R. A. (2021). Australian forests, megafires and the risk of dwindling carbon stocks. *Plant Cell Environ.* 44, 347–355. doi: 10.1111/pce.13916

Bradstock, R. A. (2010). A biogeographic model of fire regimes in Australia: current and future implications. *Glob. Ecol. Biogeogr.* 19, 145–158. doi: 10.1111/j.1466-8238.2009.00512.x

Burrows, N., and Chapman, J. (2018). *Traditional and Contemporary Fire Patterns in the Great Victoria Desert, Western Australia.* Final Report, Great Victoria Desert Biodiversity Trust Project GVD-P-17-002. Perth, WA: Biodiversity and Conservation Science Division, Department of Biodiversity, Conservation and Attractions.

Burrows, N. D., Burbidge, A. A., Fuller, P. J., and Behn, G. (2006a). Evidnce of altererd fire regimes in the Western DEsert region of Australia. *Conserv. Sci.* 5, 272–284.

Burrows, N. D., and Christensen, P. E. S. (1990). "A survey of Aboriginal fire patterns in the Western Desert of Australia," in *Fire and the Environment: Ecological and Cultural Perspectives:* General Technical Report SE-69, Southeastern Forest Experimental Station, eds S. C. Nodvin and T. A. Waldrop (Asheville, NC: U.S. Department of Agriculture Forest Service).

Burrows, N. D., Ward, B., and Robinson, A. (1991). Fire behaviour in Spinifex fuels in the Gibson Desert Nature Reserve. *Journal of Arid Environments* 20, 189–204. doi: 10.1016/s0140-1963(18)30708-0

Burrows, N. D., Ward, B., Robinson, A. D., and Behn, G. (2006b). "Fuel dynamics and fire behaviour in spinifex grasslands of the Western Desert," in *Proceedings of the Bushfire Conference 2006 Life in a Fire-Prone Environment: Translating Science into Practice*, (Brisbane QLD).

Clark, C. (2020). Causes of big bushfires in Australia: higher temperatures and rainfall or more fuel? *J. Geosci. Environ. Protection* 8, 79–94. doi: 10.4236/gep.2020.88007

Davies, S. J. J. F., and Kenny, S. A. (2013). The ages and fecundity of some arid-zone plants in Western Australia. *Rangeland J.* 35, 455–468. doi: 10.1071/rj12112

De Graaf, M. (1975). "The Aboriginal use of fire," in *Report on the Use of Fire in National Parks and Reserves, Darwin, Department of the Northern Territory Forestry, Fisheries, Wildlife, Environment and National Parks Branch*, ed. R. E. Fox 14–19.

Deb, P., Moradkhani, H., Abbaszadeh, P., Kiem, A. S., Engstrom, J., Keellings, D., et al. (2020). Causes of the widespread 2019-2020 Australian bushfire season. *Earths Future* 8:e2020EF001671. doi: 10.1029/2020ef001671

Denniston, R. F., Villarini, G., Gonzales, A. N., Wyrwoll, K.-H., Polyak, V. J., Ummenhofer, C. C., et al. (2015). Extreme rainfall activity in the Australian tropics reflects changes in the El Niño/Southern Oscillation over the last two millennia. *Proc. Natl. Acad. Sci. U.S.A.* 112, 4576–4581.

Duguid, A., Brock, C., and Gabrys, K. (2008). "A review of fire management on central Australian conservation reserves: towards best practice," in *Desert fire: Fire and Regional Land Management Practises in the Arid Landscapes of Australia*, eds G. P. Edwards and G. E. Allan (Alice Springs, NT: Desert KNowledge Cooperative Research Centre).

Ehsani, M. R., Arevalo, J., Risanto, C. B., Javadian, M., Devine, C. J., Arabzadeh, A., et al. (2020). 2019-2020 Australia fire and its relationship to hydroclimatological and vegetation variabilities. *Water* 12:3067. doi: 10.3390/w12113067

Finlayson, H. H. (1936). *The Red Centre*. Sydney, NSW: Angus and Robertson.

Gamage, B. (2012). *The Biggest Estate on Earth: How Aborigines made Australia*. Crows Nest, NSW: Allen & Unwin.

Giles, E. (1889a). *Australia Twice Traversed: The Romance of Exploration*, Vol. I. London: Sampson Low, Marsto11, Searle and Rivington.

Giles, E. (1889b). *Australia Twice Traversed: The Romance of Exploration*, Vol. II. London: Sampson Low, Marston, Searle and Rivington.

Gill, A. M. (2000). *Fire-Pulses in the Heart of Australia: Fire Regimes and Fire Management in Central Australia.* Unpublished Report to Environment Australia, August 2000.

Gill, A. M., and Allan, G. E. (2008). Large fires, fire effects and the fire-regime concept. *Int. J. Wildland Fire* 17, 688–695. doi: 10.1071/wf07145

Goforth, B. S., and Minnich, R. A. (2007). Evidence, exaggeration, and error in historical accounts of chaparral wildfires in California. *Ecol. Appl.* 17, 779–790. doi: 10.1890/06-0831

Gould, R. A. (1980). *Living Archaeology*. Cambridge: Cambridge University Press.

Griffin, G. F. (1990). Characteristics of three spinifex alliances in Central Australia. *J. Veg. Sci.* 1, 435–444. doi: 10.2307/3235776

Griffin, G. F., Price, N. F., and Portlock, H. F. (1983). Wildfires in the central Australian Rangelands, 1970-1980. *J. Environ. Manag.* 17, 311–323.

Guilliatt, R. (2010). Shcok of the new: whatever happened to the Pintupi nomads? *Weekend Austral. Magaz.*

Hansen, K. C. (1984). "Communicability of some Western Desert communilects," in *Work Papers of the SIL*-AAB Series B Language Survey, Vol. 11, eds H. Joyce and N. Pym (Nakara NT: Summer Institute of Linguistics).

Harris, S., and Lucas, C. (2019). Understanding the variability of Australian fire weather between 1973 and 2017. *PLoS One* 14:e0222328. doi: 10.1371/journal.pone.0222328

Heffernan, J. A. (1984). *Dialect Change Among the Eastern Pintupi*. Papunya, NT: Papunya Literature Production Centre.

Horn, A., and Liston, G. (2013). *Resort Evacuated as Fires Burn in Red Centre. ABC News*. Available online at: https://www.abc.net.au/news/2013-2001-2008/red-centre-heat-records-and-fires/4456544 (accessed Jan 08, 2013).

Jacobs, S. W. L. (1973). *Ecological studies on the genera Triodia R. Br. and Plectrachne Henr. in Australia.* Ph.D. thesis. Camperdown NSW: University of Sydney.

Jacobs, S. W. L. (1984). "Spinifex," in *Arid Australia*, eds H. G. Cogger and E. E. Cameron (Chipping Norton, NSW: Surrey Beatty & Sons Pty. Ltd.).

Jessop, J. (1981). *Flora of Central Australia*. Sydney, NSW: Reed Pty Ltd.

Jones, R. (1969). Fire-stick farming. *Austral. Nat. History* 16, 224–228.

Keeley, J. E., and Fotheringham, C. J. (2001). Historic fire regime in southern California shrublands. *Conserv. Biol.* 15, 1536–1548. doi: 10.1046/j.1523-1739.2001.00097.x

Keeley, J. E., and Zedler, P. H. (2009). Large, high-intensity fire events in southern California shrublands: debunking the fine-grain age patch model. *Ecol. Appl.* 19, 69–94. doi: 10.1890/08-0281.1

Keys, B., and Memmott, P. (2016). *Indjalandji-Dhidhanu Country, Qld; Cultural Heritage Survey Report, Northern Gas Pipeline. Prepared for Jemena (SGSP Assets Pty Ltd)*. Camooweal, QLD: Dugalunji Aboriginal Corporation.

Kimber, R. (1983). Black lightning: Aborigines and fire in central Australia and the Western Desert. *Archaeol. Ocean.* 18, 38–45. doi: 10.1002/arco.1983.18.1.38

Kimber, R. G., and Friedel, M. H. (2015). Challenging the concept of Aboriginal mosaic fire practices in the Lake Eyre basin. *Rangeland J.* 37, 623–630. doi: 10.1071/rj15057

Latz, P. K. (1990). *Observations on the Effect of Fire on Central Australian Grassland Communities*. Alice Springs, NT: Parks and Wildlife Commission of the Northern Territory.

Latz, P. K. (2007). *The Flaming Desert: Arid Australia – A Fire Shaped Landscape*. Alice Springs, NT: NT Print Management.

Latz, P. K. (2018). *Bushfires and Bushtucker*. Alice Springs, NT: IAD.

Letnic, M., and Dickman, C. R. (2006). Boom means bust: interactions between the El Nino/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiv. Conserv.* 15, 3847–3880. doi: 10.1007/s10531-005-0601-2

Long, J. P. M. (1971). "Arid region Aborigines: the Pintubi," in *Aboriginal Man and Environment in Australia*, eds D. J. Mulvaney and J. Golson (Canberra, NSW: Australian National University Press).

Masters, P. (1993). The Effects of Fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park. *North. Territory Wildlife Res.* 20, 803–813. doi: 10.1071/wr9930803

Matthews, D. (2005). *Fire Management – Finke Gorge National Park, Internal Report*. Alice SPrings, NT: Parks and Wildlife Service of the Northern Territory.

Memmott, P. (1992). *The Registration of a Further Sixteen Alyawarre Sacred Sites and One Wakaya Site on Elkedra Station.* Report for Aboriginal Area Protection Authority. Alice Springs, NT.

Mensing, S. A., Michaelsen, J., and Byrne, R. (1999). A 560-year record of Santa Ana fires reconstructed from charcoal deposited in the Santa Barbara Basin, California. *Quat. Res.* 51, 295–305. doi: 10.1006/qres.1999.2035

Minnich, R. A. (1983). Fire mosaics in southern California and northern Baja California. *Science* 219, 1287–1294. doi: 10.1126/science.219.4590.1287

Minnich, R. A. (1998). "Landscapes, land-use and fire policy: where do large fires come from," in *Large Forest Fires*, ed. J. M. Moreno (Leiden: Backhuys).

Moritz, M. A., Keeley, J. E., Johnson, E. A., and Schaffner, A. A. (2004). Testing a basic assumption of shrubland fire management: how important is fuel age? *Front. Ecol. Environ.* 2, 67–72. doi: 10.1890/1540-92952004002[0067:TABAOS]2.0.CO;2

Moritz, M. M., Moody, T. J., Miles, L. J., Smith, M. M., and de Valpine, P. (2009). The fire frequency analysis branch of the pyrostatistics tree: sampling decisions and censoring in fire interval data. *Environ. Ecol. Stat.* 16, 271–289. doi: 10.1007/s10651-007-0088-y

Moyle, R., and Morton, S. (1986). *Alyawarra Music: Songs and Society in a Central Australian Community*. Canberra, NSW: Australian Institute of Aboriginal Studies.

Mutitjulu community and Baker, L. (1996). *Minkiri. A Natural hisotry of Uluru by the Mutitjulu community*. Alice Springs, NT: IAD Press.

Nangala, J., Napangardi, Y., Napangardi, Y., and Wright, B. R. (2019). Ethnobotany of Warrilyu (Eucalyptus pachyphylla F.Muell. Myrtaceae): Aboriginal seed food of the Gibson Desert, Western Australia. *Econ. Bot.* 73, 416–422. doi: 10.1007/s12231-019-09471-2

Nunn, P. D., and Reid, N. J. (2015). Aboriginal memories of inundation of the Australian coast dating from more than 7000 years ago. *Austral. Geogr.* 47, 11–47. doi: 10.1080/00049182.2015.1077539

O'Connell, J. F., Latz, P. K., and Barnett, P. (1983). Traditional and modern plant use among the Alyawara of central Australia. *Econ. Bot.* 37, 80–109. doi: 10.1007/bf02859310

Rice, B. L., Westoby, M., Griffin, G. F., and Friedel, M. H. (1994). Effects of supplementary nutrients on hummock grasses. *Austral. J. Bot.* 42, 687–703. doi: 10.1071/bt9940687

Saxon, E. C. E. (1984). *Anticipating the Inevitable: A Patch-Burn Strategy for Fire Management at Uluru (Ayers Rock – Mt Olga) National Park*. Melbourne, VIC: CSIRO Australia.

Smith, M. (2013). *The Archaeology of Australia's Deserts*. Cambridge, MA: Cambridge University Press.

Southgate, R., and Carthew, S. (2007). Post-fire ephemerals and spinifex-fuelled fires: a decision model for bilby habitat management in the Tanami Desert, Australia. *Int. J. Wildland Fire* 16, 741–754. doi: 10.1071/wf06046

TERN (2019). *Summary of Sites in Hummock Grasslands 2011 - 2019*. Terrestrial Ecosystem Research Network.

Tietkens, W. H. (1890). *Journal of Mr. W.H. Tietkens' Central Australian Exploring Expedition. South Australian Parliamentary Papers*, Vol. 111. Adelaide, SA: S.A. Government Printer, 2–32.

Tjupurrula, J. Y. (2014). *Tjukurrpa Ngaatjanya Maru Kamu Tjulkura (Dreaming In Black And White)* [Online]. ReDot Fine Art Gallery. Available online at: https://issuu.com/redotfineartgallery/docs/20121017_tjukurrpa_ngaatjanya_maru_ (accessed January 29, 2021).

Turner, D., Ostendorf, B., and Lewis, M. (2008). An introduction to patterns of fire in arid and semi-arid Australia, 1998–2004. *Rangeland J.* 30, 95–107. doi: 10.1071/rj07039

Verhoeven, E. M., Murray, B. R., Dickman, C. R., Wardle, G. M., and Greenville, A. C. (2020). Fire and rain are one: extreme rainfall events predict wildfire extent in an arid grassland. *Int. J. Wildland Fire* 29, 702–711. doi: 10.1071/wf19087

Vitaliano, D. (1973). *Legends of the Earth: Their Geologic Origins*. Bloomington, IN: Indiana University Press.

Warburton, P. E. (1875). *Journey Across the Western Interior of Australia*. London: Sampson Low, Marston, Low & Searle.

Winkworth, R. E. (1967). Composition of several arid spinifex grasslands of central Australia in relation to rainfall. *Austral. J. Bot.* 15, 107–130. doi: 10.1071/bt9670107

Wright, B. R. (2007). *Fire Ecology of the Spinifex Hummock Grasslands of Central Australia.* Ph.D. thesis. Armidale, NSW: University of New England.

Wright, B. R. (2018). Evidence that shrublands and hummock grasslands are fire-mediated alternative stable states in the Australian Gibson Desert. *Oecologia* 188, 525–535. doi: 10.1007/s00442-018-4215-2

Wright, B. R., and Clarke, P. J. (2007). Fire regime (recency, interval and season) changes the composition of spinifex (Triodia spp.)-dominated desert dunes. *Austral. J. Bot.* 55, 709–724. doi: 10.1071/bt06240

Wright, B. R., and Clarke, P. J. (2008). Relationships between soil temperatures and properties of fire in feathertop spinifex (*Triodia schinzii* (Henrard) Lazarides) sandridge desert in central Australia. *Rangeland J.* 30, 317–325. doi: 10.1071/rj07049

Wright, B. R., and Clarke, P. J. (2009). Fire, aridity and seed banks. What does seed bank composition reveal about community processes in fire-prone desert? *J. Veg. Sci.* 20, 663–674. doi: 10.1111/j.1654-1103.2009.01051.x

Wright, B. R., and Fensham, R. J. (2017). Fire after a mast year triggers mass recruitment of slender mulga (*Acacia aptaneura*), a desert shrub with heat-stimulated germination. *Am. J. Bot.* 104, 1474–1483. doi: 10.3732/ajb.1700008

Wright, B. R., and Fensham, R. J. (2018). Fire-timing in relation to masting: an important determinant of post-fire recruitment success for the obligate-seeding arid zone soft spinifex (*Triodia pungens*). *Ann. Bot.* 121, 119–128. doi: 10.1093/aob/mcx136

Wright, B. R., Zuur, A. F., and Chan, G. C. K. (2014). Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. *Rangeland J.* 36, 297–308. doi: 10.1071/rj13104

Yates, P., and Morse, J. (2003). *Anangu/Pitjantjatjara/Yankunytjatjara Lands Fire Management Strategy. Unpublished Report to Anangu Pitjantjatjara-Yankunytjatjara Land Management, Umuwa.*

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Climate Impacts on Fire Risk in Desert Shrublands: A Modeling Study

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Fire is recognized to be an important disturbance in many ecosystems worldwide, although desert ecosystems are not generally thought of as being prone to fire, primarily because of the lack of a continuous fuel bed. However, the likelihood of catastrophic fires in some desert systems is increasing due to the spread of exotic species, which can grow in the open. A second factor increasing fire risk may be extreme rainfall events caused by climate warming that can lead to an increase in fuel loads. Our work explores the impact of increased rainfall on fire risk in creosote shrublands that have been invaded by exotic grasses. We take experimental results from creosote (*Larrea tridentata*) shrublands in the Mojave and Sonoran Deserts of the Southwestern United States and develop spatially explicit simulation models to explore the impact of shifting rainfall regimes on biomass production and fire spread. In doing this, we explore two scales that are important in the spread of fire: (1) the macro-scale which considers the likelihood that fire arriving at one edge of a modeled landscape will successfully reach the opposite edge, leading to spread at a broader scale; and (2) the micro-scale, which considers fire spread within the landscape. We use a very simple model to first explore how changes in the distribution of fuel in the landscape impact the ability of fire to spread across and within the landscape. We then add more realism by including a direct consideration of creosote shrub distributions and biomass levels produced in different vegetation zones associated with distance from creosote. Our models show that the spread of fire at both macro- and micro-scales can be predicted from a knowledge of the statistical distribution of biomass in the field. The only additional information that is needed to predict the extent of fire spread is the amount of biomass at a local site ($g\ m^{-2}$) required to ignite standing biomass in adjacent sites. This will depend upon species composition as well as amount of biomass, the hydration status of the vegetation and climatic conditions, such as windspeed and relative humidity.

Keywords: creosote, simulation, percolation, fire, Mojave, Sonoran, climate change, exotic invasive species

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INTRODUCTION

Fire is recognized to be an important disturbance in many ecosystems worldwide. It can alter vegetation structure, soil properties, and other key ecosystem functions (Whelan, 1995; Sugihara et al., 2006). Many ecosystems on Earth, though, are naturally dependent on wildfires. About 4% of global land surface burns on an annual basis (Randerson et al., 2012). To date, a great deal of the literature has focused on explaining how fire regimes are changing around the globe due to climate change (see Grissino Mayer and Swetnam, 2000; Cary, 2002; Bowman et al., 2009), spread of exotic species, historical fire suppression and human-induced fire. In fact, it has been shown that the incidence of fire has increased in the past 2000 years and human-impact in prehistorical and historical time has favored fire outbreaks around the globe (Marlon et al., 2008; Wang et al., 2010).

Desert ecosystems are not generally thought of as being prone to fire, primarily because of the lack of a continuous fuel bed to carry fire (Brooks and Matchett, 2006; Allen et al., 2011; Fuentes-Ramirez et al., 2016). However, changes in rainfall regimes, spread of invasive species and an increase in human activity may be leading to enhanced fire risk in these systems through an increase in connectivity of the fuel bed during high rainfall years (Moloney et al., 2019). As a consequence, native desert species may be at risk as they are poorly adapted to fire due to the low historical fire frequency. In desert regions of southwestern North America (e.g., the Mojave and Sonoran deserts), native herbaceous plant communities are less diverse in burned compared to unburned areas (Brooks, 2002; Engel and Abella, 2011), and desert shrubs, such as the creosote bush, *Larrea tridentata* (DC.) Cov. (Zygophyllaceae; hereafter *Larrea*) are very fire sensitive. *Larrea* is a slow-growing, deep-rooted, and long-lived (up to 11,700 year; Vasek, 1980) shrub that is uniquely adapted to survive intense droughts, but not fire (post-fire resprouting rate of 3–30%; Abella, 2009).

Over the last several decades, the Mojave and Sonoran deserts in the Southwestern US have been invaded by exotic grasses (e.g., *Bromus* and *Schismus* species) and forbs (e.g., *Erodium cicutarium* and *Brassica tournefortii*; D'Antonio and Vitousek, 1992; Brooks et al., 2004), which has increased the susceptibility of these deserts to fire. The abundance of exotic invasive species is often closely tied to seasonal and annual variation in precipitation, which may lead to greater biomass production and fuel loads within the inter-shrub areas during periods of above average rainfall; whereas, prior to invasion, these systems tended to have low fuel loads in the inter-shrub areas even after periods of high rainfall (Bradley et al., 2016). As a consequence, fire risk is often greater after rainy seasons with above-average rainfall in invaded systems, because of greater plant growth and litter production, which can fuel larger fires (Brooks et al., 2004; Chambers and Wisdom, 2009; Esque et al., 2013; Moloney et al., 2019). By serving as spreaders of fire, exotic annual grasses in particular have transformed these deserts through fire-induced mortality of keystone shrubs and reduction of the high soil nutrient availability, typically associated with fertility islands (Mudrak et al., 2014; Fuentes-Ramirez et al., 2015a,b). Thus, where invasive grasses are abundant, shrub islands are prone to burn (Brooks, 2002), strengthening the grass-fire cycle long known to drive fire incidence in invaded ecosystems (D'Antonio and Vitousek, 1992).

Within this context, we designed a multiyear experimental study exploring the responses of annual plant communities to increased precipitation in *Larrea* dominated shrub desert landscapes of the Sonoran and Mojave deserts (Schafer et al., 2012; Moloney et al., 2019). The focus was on understanding the spatial distribution of fuel as a function of shrub locations. For example, the well-known, nutrient-island effect of creosote shrubs leads to a concentration of nutrients under shrubs with nutrient levels falling off with distance from shrubs (Charley and West, 1975; Schlesinger et al., 1996; Thompson et al., 2005; Ewing et al., 2007; Mudrak et al., 2014). Related to this, it has been thought that the increased fire risk in creosote shrublands (primarily through studies in the Mojave) is enhanced by invasive annuals that can grow in the open unlike native species, which grow best under the shrub canopies and are only sparsely distributed in the open (Brooks et al., 2004; Brooks and Matchett, 2006; Fuentes-Ramirez et al., 2016). Our experiment showed that with increased precipitation, biomass increased significantly in both the Mojave and Sonoran sites and was highest under shrubs, decreasing with distance into the open matrix as predicted (Moloney et al., 2019). What may be most critical for fire spread is the change in biomass in the open matrix as there needs to be enough fuel to carry fire from shrub to shrub (Fuentes-Ramirez et al., 2016). In **Figure 1** you can see evidence of these relationships from a fire caused in the Mojave by an exploding electrical transformer.

One goal of our research project was to use data from the experimental study to develop a spatially explicit simulation model examining the impact of increased precipitation on fire risk in the two desert systems. The work discussed here presents the results of a modeling study based on these data. In analyzing the model, we examined two aspects of fire spread representing two scales of the process. At the regional scale, we considered the broad scale spread of fire through the landscape. The critical element of this process is that the spatial distribution of fuel is sufficient to allow fire to bridge a landscape element and spread fire to adjacent areas of the landscape. At the local scale, we considered the amount of spread within a landscape element after ignition of fire at a single point in the landscape. Critical here is the proportion of the landscape burned from a single ignition point. This represents the risk of fire damage to the local plant community. Ultimately, we hope to provide valuable insights for fire management in deserts. In particular, we aim to arrive at estimates of biomass thresholds above which fire can spread through desert landscapes. Information on such thresholds can provide a determination of critical fuel loads, such as ones built up by the growth of invasive, exotic grasses after extreme rainfall events that could lead to destructive fires.

MATERIALS AND METHODS

In developing the fire simulation model, we began with a very basic, binary landscape characterizing only two types of habitat, flammable and non-flammable, distributed at random. More "realistic" detail was then added to the model to explore the impact on the spread of fire by: (1) the differential likelihood of ignition of neighboring cells from a burning cell; (2) the presence of shrubs; and (3) patterns of biomass distribution based on field observations and precipitation experiments. Our philosophy in applying this approach derived from the belief that the best approach to understanding complex phenomena is to develop an

FIGURE 1 | Creosote shrubland fire on Fort Irwin Army Base, California in June of 2011. The fire was started by an exploding electrical transformer. The big fire scars seen in the photo are due to higher biomass of annual plants under creosote. The fire in the annuals was clearly hot enough with enough duration to burn the creosote stems. There is evidence of fire spread in the matrix in the right foreground where there is blackened plant material in the open. Photo by Kirk A. Moloney.

understanding of the basic building blocks of the process before adding more realistic detail.

Field Data

Field data for the model experiments were required to parameterize annual plant biomass distributions used in determining the spatial distribution of fuel loads in the model landscapes (see below). These data were obtained from an experimental study conducted from 2011 to 2013 at two sites in the Southwestern US (Schafer et al., 2012; Moloney et al., 2019). One site was in the Mojave Desert and the other in the Sonoran.

The Mojave Desert site (35°9′021″ N, 116°53′6″ W, 865 m MSL) was located within the Fort Irwin National Training Center, north of Barstow, California. The average annual precipitation is 147 mm with a mean annual temperature of 17.7°C (data from the Goldstone Echo 2 weather station 22 km N of our study site, Western Regional Climate Center)[1]. Precipitation at this site is predominantly from winter rains. The study site was located on an east-facing bajada dominated by *L. tridentata* (DC.) Cov. and *Ambrosia dumosa* (A. Gray) Payne. Soils are young and intermediate aged alluvial grus (decomposed granite; Amoroso and Miller, 2006).

The Sonoran Desert site (32°41′49″ N, 112°50′22″ W, 322 m MSL) was located within the Barry M. Goldwater Range, south of Gila Bend, Arizona. It has an average annual precipitation of 153.9 mm and mean annual temperature of 22.7°C [data was from the Gila Bend weather station, 29 km NNE of our study site, Western Regional Climate Center (see text footnote 1)]. The Sonoran site is characterized by two wet seasons with rainfall during both the summer and winter. As in the Mojave site, *Larrea* is the dominant species; however sub-dominant shrub species are mostly lacking. Soils were coarse-loamy, hyperthermic, typic hyplicalcids (U.S. Department of Agriculture)[2].

The methodology and rationale for the experimental study have been reported in detail in Schafer et al. (2012) and Moloney et al. (2019). The pertinent component of the experimental protocol for this paper is that peak annual biomass was determined for 1,344, 20 × 20 cm permanent microplots that differed in distance to the base of *Larrea* shrubs. Biomass was determined with non-destructive methods from measures of percent aerial cover (*cov*) and height (*h*) in cm. These two quantities were regressed against dry biomass ($g/100\ \text{cm}^2$) harvested from comparable microplots in adjacent areas at each site during each year of the study (for details see Appendix S3 of Moloney et al., 2019). The resulting equations were used to determine biomass in the microplots each year.

The permanent microplots were located relative to 168 randomly chosen creosote shrubs within an 83 × 130 m

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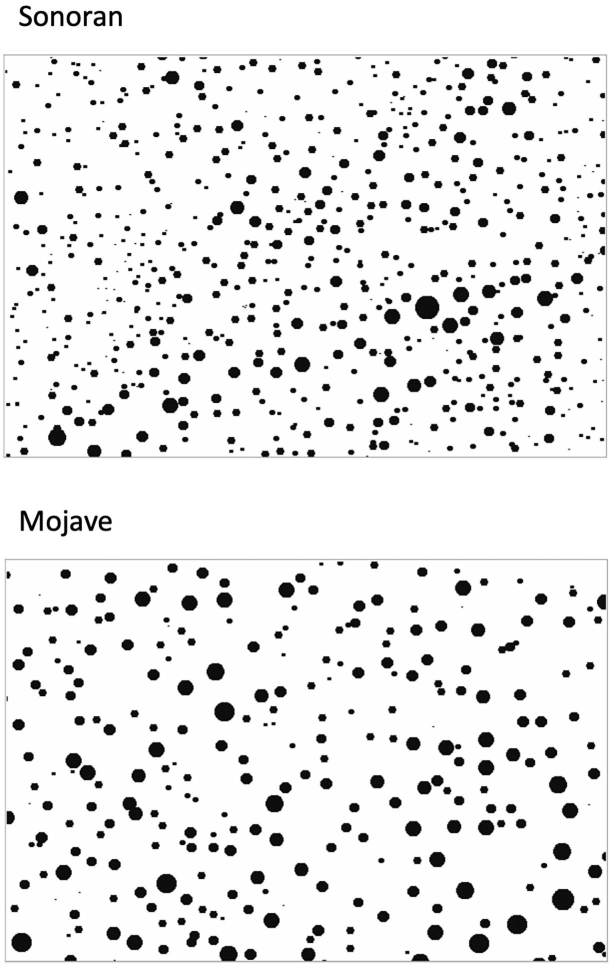
[1] http://www.wrcc.dri.edu

[2] http://soildatamart.nrcs.usda.gov

experimental plot in each desert site. The positions chosen for the microplots were used to represent four major micro-habitats associated with the "nutrient island" effect in creosote shrublands (Garcia-Moya and McKell, 1970; Schlesinger et al., 1996; Mudrak et al., 2014). The four micro-habitats were: (1) under-the-canopy (UC); (2) canopy drip-line (CD); (3) open, near-to-shrub (ON); and (4) open, far-from-shrub (OF). Details on the placement of the microplots relative to shrubs can be found in Moloney et al. (2019) and Schafer et al. (2012). Annual plants tend to produce more biomass in creosote influenced UC and CD habitats with the amount tapering off in ON and OF habitat with the trend in density being the opposite (Moloney et al., 2019). The proportion of native vs. exotic annuals was also much higher at the Sonoran site than the Mojave (Moloney et al., 2019).

In the winter of 2010–2011 data were obtained from replicates of the four microhabitats. Immediately after data collection, we introduced four different treatments applied in a split-plot, factorial design: (1) burned vs. unburned; (2) soil turbation vs. unturbated; (3) seed addition vs. no seed addition; and (4) precipitation with three levels of moisture (1/2 ambient, ambient and 2× ambient rainfall). In this paper we will only be using data from the unburned, unturbated, and 2× ambient precipitation treatment (highest moisture level) to parameterize simulations. Since seed addition had no effect on outcomes, we pooled replicates from both seed treatments in our analyses. The high moisture treatment (2× ambient) was designed to mimic approximately double the amount of ambient precipitation during 2012 and 2013 by adding hand irrigation and represents the conditions producing the highest risk of fire spread due to increased biomass production by annual plants. Burn and disturbance treatments had a minimal experimental effect on biomass, particularly when compared to the effects of precipitation, so we did not consider data from these treatments in our models. For complete details of the experimental design see Moloney et al. (2019).

Shrub size and location data for both experimental sites were obtained as described in Mudrak et al. (2014). We modeled the horizontal profile of shrubs using canopy area as described in Mudrak et al. (2014), converting the oval shape of the canopy to circular areas maintaining the same cover area (**Figure 2**).


Sonoran

Mojave

FIGURE 2 | Creosote maps used in the simulation program for the Sonoran and Mojave experimental plots based on field surveys. Both sites are 120 × 80 m, length vs. height respectively.

Simulation Model

General Model Structure

The simulation model was written in C++ and is hierarchical in nature, comprising three fundamental layers: (1) the landscape, which defines the extent of the model through two parameters $\{w,h\}$, width and height in meters, respectively; (2) a raster-based layer composed of a matrix of 20 × 20 cm cells containing annual plants; and (3) a vector-based layer, which represented shrubs. The raster-based layer comprises a matrix of cells with each cell's state characterized by the cell's flammability and ability to spread fire to adjacent cells. An individual cell c_{ij} is referenced by its {i,j} location in the matrix.[3] The vector-based layer contained shrubs. Each shrub was defined by three parameters $\{x, y, r\}$; x and y coordinates represent the shrub's geographic center of biomass in the landscape and r is the radius of the shrub canopy. Before running fire simulations, shrubs were converted to a raster layer containing all cells whose centroids fell inside circles of radius r centered on locations $\{x,y\}$ for all shrubs (see **Figure 2**). This layer was then used to modify the flammability of the annual plant matrix layer.

Cell Flammability State

The flammability state of a cell c_{ij} located at landscape position $\{i, j\}$ was characterized by two parameters, the probability that the cell could burn (f_{ij}) and the probability that a burning cell spreads fire to a neighboring cell (s_{ij}). Cell flammability was set in two different ways depending upon the modeling approach:

Simple Binary Landscapes

In binary landscapes cells in the model were randomly set as being either flammable ($f_{ij} = 1$) or non-flammable ($f_{ij} = 0$) with a probability p_{cell}. In this case, for each cell c_{ij} in the model landscape the flammability state was set by obtaining a random

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[3] **Table 1** provides definitions of the mathematical symbols used to represent variables in the paper as a quick reference.

TABLE 1 | Definitions of variables used in the model and analyses.

Variable	Definition
b_{ij}	Biomass contained in c_{ij}
c_{ij}	Cell located at position {i,j}in the landscape.
Δ	Biomass cutoff threshold in g m^{-2}. If $b_{ij} < \Delta$ then the cell cannot ignite adjacent cells. If $b_{ij} \geq \Delta$ and the cell is burning, it can spread fire to adjacent cells.
f_{ij}	Flammability of c_{ij}. If $f_{ij} = 1$ the c_{ij} can burn; if $f_{ij} = 0$ the cell cannot burn.
p_{cell}	Probability in a binary model that a randomly chosen cell will be flammable
s	Probability of spread, i.e., the probability that a burning cell will ignite an adjacent flammable cell.
$p_{crit=0.5928}$	Critical p_{cell} value above which an infinite binary landscape will percolate (see text for a definition of percolation).
{x, y, r}	Location and radius of a shrub in the landscape: x is the horizontal location; y is the vertical location; and r is the radius of the shrub.
{w,h}	Landscape dimensions: w is horizontal width h is vertical height

number (n) from a uniform probability distribution on the unit interval, if $n \leq p_{cell}$ then $f_{ij} = 1$, otherwise $f_{ij} = 0$.

Realistic Landscapes

Cells were first populated by setting the biomass of annual plants in each cell (b_{ij}) in the landscape, with b_{ij} being the biomass in cell c_{ij}. The method for determining biomass depended on the model experiment being conducted (see below). Once biomass was set, the flammability of a cell was set to zero if no biomass was present, otherwise $f_{ij} = 1$. The probability that fire could spread from a burning cell to adjacent cells was a function of biomass determined by a cutoff value (Δ) set for a model simulation run. In the simple case explored in this paper, if $b_{ij} \geq \Delta$ then $s_{ij} = 1$, otherwise $s_{ij} = 0$.

Fire Initiation

Fire was initiated in a simulation in one of two ways, depending upon the experiment. In experiments exploring *percolation-spread* (i.e., macro-scale fire spread), all cells along one edge (the southern edge) were ignited at the start of a simulation. In *point-spread* experiments (i.e., micro-scale fire spread), fire was initiated at a single, randomly selected cell within the landscape.

Fire Spread

Fire in a burning cell c_{ij} ignited a neighboring cell if a random number (n) drawn from a uniform probability distribution on the unit interval was less than or equal to the probability of spread s_{ij}. Fire spread from a burning cell was determined in this fashion for all neighboring cells. Cell neighborhoods for fire spread were defined either as the four cells lying in the four cardinal directions adjacent to a focal cell (von Neumann neighborhood) or as the eight cells surrounding the focal cell (Moore neighborhood). Exploratory experiments comparing spread for the two neighborhood types showed that there was little difference in the qualitative pattern of fire spread (results not shown). As a consequence, we only explore models using a von Neumann (4 cell) neighborhood in this paper.

Model Run End State

Model runs ended at the point where there was no more spread of fire. The outcome of the model was assessed differently depending upon the way the model was initiated.

Percolation-Spread (Macro-Scale)

In each percolation-spread model run, the output was examined to determine if any cell on the northern border had burned after all the cells on the southern border were ignited. If at least one cell on the northern border burned then the model had successfully "percolated." Successful percolation indicated that there was at least one path of flammable cells leading from the southern edge to the northern edge of the model landscape. A landscape that percolates can carry a fire across the local landscape and can act as a conduit of fire within a broader landscape. Landscapes that do not percolate can't spread fire between adjacent landscape elements.

One key benchmark for assessing percolation is what is known as the p_{crit} value, which is equal to approximately 0.5928 (Gardner et al., 1987; Cox and Durrett, 1988). This is a theoretical quantity that represents a threshold value for a theoretically infinite 2-dimensional landscape composed of cells. If the proportion of cells in an infinite landscape that are flammable is less that p_{crit} then there is no available continuous path for fire to cross the landscape. If the proportion of traversable cells is greater than p_{crit} then it is guaranteed that there is at least one traversable path. For landscapes that are not infinite the likelihood of percolation across the landscape is still related to p_{crit} but in a more nuanced fashion as we explore in experiment E-1 below (also see Abades et al., 2014).

Point-Spread (Micro-Scale)

We determined the proportion of flammable cells in the landscape that burned as well as the proportion of all landscape cells that burned. This provided an assessment of the extent of fire spread within the local landscape from an initial ignition point originating in the landscape.

Simulation Experiments

Simple Binary Landscapes

Our first experiments in developing the fire model were designed to explore the dynamics of spread in a very simple system before adding more realism. For these experiments, cells in the landscape were set to one of two states, flammable or not flammable as explained above. All analyses involving simple binary landscapes, with the exception of E-1, were conducted on 80 m x 40 m landscapes, i.e., 400 × 200 cells, somewhat smaller than the approximate scale of the experimental sites motivating the model.

Landscape Scale Experiment [E-1]

In the first experiment, we varied landscape scale to explore how this would impact realized percolation probabilities for different landscape sizes with the same underlying p_{cell} values. The smallest landscape was 200 × 100 cells (40 × 20 m). We doubled the size of the landscape up to a maximum value of 12,800 × 6,400 cells (2,560 × 1,280 m) for a total of 7 landscape sizes.

Before conducting model runs at each landscape scale, we used a coarse scale search at low p_{cell} values, i.e., lower than $p_{crit} = 0.5928$, to determine p_{cell} values below which fire never percolated across the landscape. We used the same process to determine values above p_{crit} for which fire always percolated. Once the upper and lower bounds were determined we varied p_{cell} in increments of 0.002 between the lower and upper bounds. At each parameter setting we generated 100 random landscapes and conducted a percolation-spread analysis on each.

Probability of Spread Experiment [E-2]

As in experiment E-1, cells were randomly set to be either flammable or non-flammable using the same protocols for setting p_{cell} values as in E-1. The probability that a cell could ignite another cell in the same neighborhood (s) was systematically altered between values of 0.5 and 1.0 in increments of 0.1 and the same value was applied to all cells of a replicate landscape. One hundred replicate runs were produced for each parameter combination of p_{cell} and s and each replicate was examined to see if it percolated.

Point-Spread Experiment [E-3]

In this experiment, p_{cell} and s values were varied over the same range of values as described in E-2. We will only report results for model runs with s = 1.0 as this captures the qualitative nature of the process at all values of s. As before, 100 replicates were run for each parameter value combination. In each model run fires were initiated by randomly setting one cell on fire and then fire was allowed to spread following the normal rules. This allowed us to explore the range of variability in fire spread due to differences in local conditions (e.g., **Figure 3**).

Shrub as Firebreak or Accelerant Experiment [E-4]

Three sets of experiments were conducted to explore the impact of shrubs occurring in the landscape on resulting fire spread: (1) no shrubs—as in the previous experiments; (2) shrubs that burned—potentially acting as an accelerant to fire spread; and (3) shrubs that don't burn—potentially acting as a fire break. We can view this simplistic depiction of the impact of shrubs as a proxy for the effect shrubs have on the fuel loads under their canopies. They act as an accelerant under dry conditions when shrubs lead to high fuel loads under their canopies. In contrast, inhibition could be caused by low fuel loads under shrubs or high moisture levels lowering the flammability of the fuel bed. These experiments were explored using the percolation-spread fire model.

For each of the three experiments in E-4, binary landscapes were constructed as in E-2 across a range of p_{cell} values holding spread (s) constant at a value of 1.0. One hundred replicates of each parameter combination were used for each of the three experiments. For models including shrubs, a random set of shrubs were produced based on the characteristics of creosote shrubs found at the Mojave Desert experimental site (unpublished analysis). The distribution of shrubs was modeled as a Strauss process with a beta of 0.031 and hard separation distance of 3.15 m using the routine rStrauss from the spatstat package in R (Baddeley et al., 2015). [The average distance between creosote shrubs at the Mojave site was 3.15 m (Mudrak et al., 2011).] This produced an average of 0.028 shrubs per m^2 in a 40 × 20 m landscape (90 shrubs total on average per landscape). This was close to the value observed in the field of 0.031 shrubs m^2. Once the shrub locations were determined their sizes were randomly assigned using a mean radius of 0.97 m (standard deviation = 0.408), the same distribution as observed for the 301 shrubs measured at the Mojave site. The cell locations covered by shrub canopies were all set to a value of f = 1 in models with shrubs acting as an accelerant and were set to f = 0 with shrubs acting as fire breaks. These experiments were explored using the percolation-spread fire model.

Realistic Landscapes

The preceding experiments all took place on a simple binary landscape to develop an understanding of fire spread in a context that was easy to interpret. In the "realistic" landscape experiments we built in more detail about the general desert shrub system to

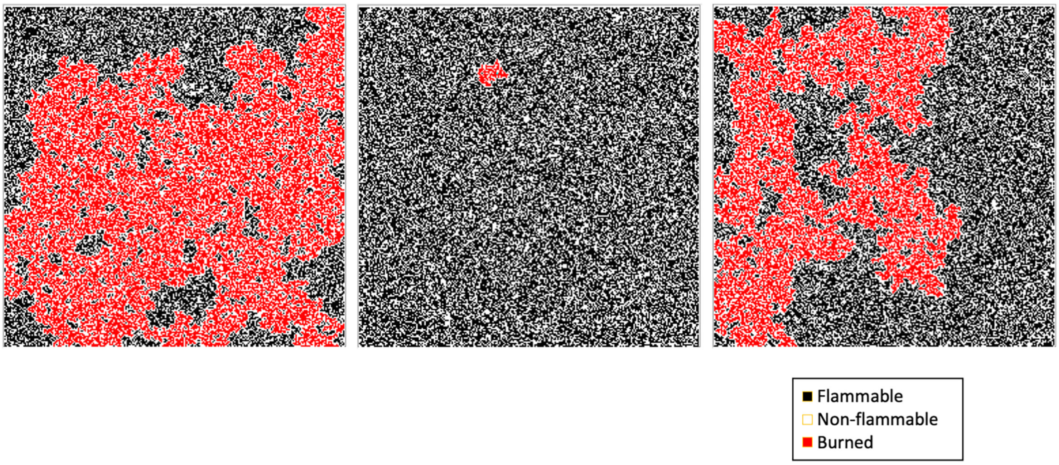

FIGURE 3 | Three replicates of random-point ignition in 250 × 250 cell binary landscapes with fixed values of $p_{cell} = 0.60$ and $p_{spread} = 1.00$.

explore the impact on fire spread. In this case, experiments were conducted on a 120×80 m landscape. Realism was added in two steps. First we made the matrix habitat more realistic by modeling biomass based on gamma probability distributions associated with the OF habitat, i.e., the habitat not influence by the presence of shrubs (see Chen et al., 2008, for a discussion of the gamma distribution as an appropriate model for biomass distributions of plants). In a second step, we added more realism by including the effects of shrubs on the distribution of annual plants due to the shrub island effect. This was done by characterizing the microhabitats of cells as being a function of distance from shrubs.

Gamma distribution parameters for specific microhabitat conditions (i.e., microhabitat location and experimental treatment) were determined in a two-step approach analyzing the experimental data corresponding to conditions of the 4 experimental microhabitats using a Hurdle model. In the first step we determined the probability that a sample for the specific conditions under consideration had measurable biomass (p_{occ}). We then determined the rate and shape parameters for the gamma distribution using the *glm* in R with a log-link function (R Core Team, 2019). Only replicates including measurable biomass were included in the latter analysis. The results of these analyses are shown in **Tables 2**, **3**.

In all of the experiments modeling biomass as a fuel, we determined the biomass of annuals in each cell of the landscape in two steps using a Hurdle model as in the analysis of the experimental data. First, we determined if the cell was empty or contained measurable biomass based on the probability distribution that a cell had a measurable amount of biomass (**Tables 2**, **3**; *Probability occupied*). In each cell containing biomass, a biomass value (b_{ij}) was randomly drawn from a gamma distribution using the boost libraries for C++ (boost.org, 2014). The gamma is a two parameter distribution determined by shape and rate (Bolker, 2008). The parameters used to determine biomass in each cell were based on the empirical values associated with the microhabitat being modeled (**Table 3**).

Biomass-Matrix Percolation Experiment [E-5]

We used parameters based on the microhabitat farthest from shrubs (OF) to determine cell biomasses (**Table 3**). The experiment was designed to explore a matrix only landscape, i.e., one devoid of shrub effects.

We examined two scenarios based on observed biomass distributions in our field experiments. The first scenario was for the Mojave site in 2013 and second for the Sonoran site in 2012. In both cases we used parameters obtained for the high-moisture (2× ambient precipitation) treatment. These years were the best growth years in the sites for which we collected biomass data with the high-moisture treatments producing the greatest amount of biomass (**Table 2**).

In both experiments we altered a biomass threshold variable (Δ) to vary the conditions under which fire could spread. A cell with $b_{ij} < \Delta$ could not spread fire to neighboring cells but can burn, i.e., $s_{ij} = 0$ and $f_{ij} = 1$, respectively. Any cell with $b_{ij} \geq \Delta$

TABLE 2 | Biomass values for matrix microhabitat (OF) fit to a gamma distribution from the experiments conducted in the Mojave and Sonoran deserts.

			Gamma parameters				
Desert	**Year**	**Water treatment**	**Rate**	**Shape**	**Probability occupied**	**Mean biomass (g m^{-2})**	**Biomass threshold (g m^{-2})**
Mojave	2011*	High	0.694	1.189	0.893	42.850	17.512
		Ambient	1.021	1.384	0.893	33.890	15.328
		Low	0.779	1.370	0.923	44.000	21.716
	2012	High	127.335	2.472	0.607	0.485	0.062
		Ambient	34.700	1.527	0.179	1.100	NA
		Low	0.000	0.000	0.000	0.000	NA
	2013	High	2.017	3.413	1.000	42.313	33.418
		Ambient	3.548	2.120	0.964	14.935	9.859
		Low	NA	NA	0.143	0.554	NA
Sonoran	2011*	High	0.00	0.00	0.04	2.50	NA
		Ambient	2.31	0.91	0.14	9.88	NA
		Low	0.00	0.00	0.07	1.00	NA
	2012	High	0.83	1.44	1.00	43.28	27.01
		Ambient	0.40	0.60	0.96	37.38	10.99
		Low	4.37	0.41	0.93	2.33	0.30
	2013	High	4.26	3.86	1.00	22.63	18.24
		Ambient	6.67	3.94	1.00	14.78	11.96
		Low	9.11	2.33	0.71	6.40	2.17

*Biomass threshold is the minimum biomass value that will produce enough 20 cm× 20 cm cells (greater than p_{crit}) to allow fire to percolate across the landscape if biomass is distributed randomly. The latter values take into account the proportion of sites that are not occupied in making the calculation. All estimates were based on 28 replicate samples with the exception of the low water treatment which had 14 replicates. Note that the parameters for the gamma distribution were fit to biomass values in 0.04 m^2 microplots, but we have converted biomass values for the mean and threshold to equivalent m^2 units in the table, i.e., values produced from the distribution were multiplied by 25. * 2011 values come from samples that were obtained before treatment conditions were applied.*

TABLE 3 | Biomass values fit to a gamma distribution from the experiment conducted in the Mojave and Sonoran deserts.

			Gamma parameters				
Desert	**Year**	**Microhabitat**	**Rate**	**Shape**	**Proportion occupied**	**Biomass (g m^{-2})**	**Biomassthreshold (g m^{-2})**
Mojave	2013	UC	0.598	0.621	0.821	67.772	26.832
		CD	1.156	0.158	1.000	68.277	53.158
		ON	2.972	0.415	1.000	53.955	46.484
		OF	2.017	3.413	1.000	42.313	33.418
Sonora	2012	UC	0.59	1.75	0.96	74.62	46.05
		CD	1.12	2.94	1.00	65.82	50.52
		ON	1.09	2.31	1.00	52.87	38.42
		OF	0.83	1.44	1.00	43.28	27.01

All replicates were from high precipitation (E), unburned (UB) and undisturbed (N) treatments during years of greatest growth in the experiment, i.e., 2013 and 2012 for the Mojave and Sonoran experimental sites, respectively. Biomass threshold is the minimum biomass value that will produce enough 20 cm × 20 cm cells (greater than p_{crit}) to allow fire to percolate across the respective microhabitats, if biomass is distributed randomly. The latter values take into account the proportion of sites that are not occupied in making the calculation. All estimates were based on 28 replicate samples. Note that the parameters for the gamma distribution were fit to biomass values in 0.04 m^2 microplots, but we have converted biomass values for the mean and threshold to equivalent m^2 units in the table, i.e., values produced from the distribution were multiplied by 25.

could spread fire to an adjacent cell (and can burn). The only cells that can't burn are those that don't have any biomass, i.e., $b_{ij} = 0$. The spread of fire from one cell to another was determined as in the binary landscape experiments. In all model runs for this experiment we used a percolation fire model. High and low values of Δ were determined as in the binary landscape experiment. We then changed Δ in increments of 0.005 (g per 0.04 m^2) from the low to high value producing 100 replicates at each parameter combination (Note that the results are reported in g m^{-2}).

Shrub-Island Experiments

In the shrub-island experiments, four different habitat zones were defined for the models based on the location and size of shrubs (**Figure 4**). These zones corresponded to the microhabitat treatments of the experiments in the Mojave and Sonoran Deserts. As in the previous experiment, two different models were used based on high-water treatments from the Mojave and Sonoran sites in 2013 and 2012, respectively. Cell biomasses were determined as in the previous experiment with the addition of considering microhabitat type in setting the probabilities for each cell (**Table 3**). We conducted two experiments using two different types of fire regime. In the *percolation experiment [E-6]*, fire was initiated as in the other experiments exploring percolation fire spread. In the *point-spread experiment [E-7]*, fire was initiated as in experiment E-3. In both experiments we varied the biomass threshold variable (Δ) in increments of 0.01 (g per 0.04 m^2) producing 100 replicates at each parameter combination (Note that the results are reported in g m^{-2}).

Statistical Analyses

All statistical analyses were conducted in R (R Core Team, 2019).

Fitting Percolation Probability Curves

Percolation probability curves for an experiment were determined using *glm* with a binomial-link function. Each model replicate either percolated or didn't percolate. This result was regressed using p_{cell} for binary landscapes and Δ for landscapes produced using gamma distributions for determining biomass levels in cells.

Calculating Threshold Biomass Values for Fire Percolation

We calculated the **biomass threshold value** (*threshold*) for fire spread for each set of microhabitat conditions using the R formula *threshold* = *qgamma* (p_{occc} – p_{crit}, *shape*, *rate*). The biomass threshold value represents the cut point for percolation in an infinite landscape given the probability conditions of the microhabitat under consideration. If the amount of biomass required to spread fire to neighboring cells lies above the biomass threshold value for a specific landscape the fire cannot percolate. If the amount required is less than the threshold value, then there is the potential for the fire to percolate conditional on the size of the landscape considered. The quantity $p_{\text{occ}} - p_{\text{crit}}$ adjusts for the probability that some cells may not have any measurable biomass, i.e., $p_{\text{occ}} < 1.0$. If $p_{\text{occ}} \leq p_{\text{crit}}$ then fire cannot percolate across the landscape under any circumstances.

RESULTS

Simple Binary Landscape Experiments

Landscape Scale Percolation Experiment [E-1]

The slope of the percolation probability curve estimated from model runs for different landscape scales steepens in the transition from a probability of zero to a probability of one as landscapes become larger (**Figure 5**). Also, the range of landscape values between the lower bound of no percolation and the upper bound of always percolating narrows as landscape scale increases. This is consistent with the theoretical result for infinite landscapes which produce a step function of no percolation with p-values below p_{crit} and certain percolation above p_{crit}. Interestingly, the curves for the landscapes of different size intersect close to the p_{crit} value on the x-axis (**Figure 5**).

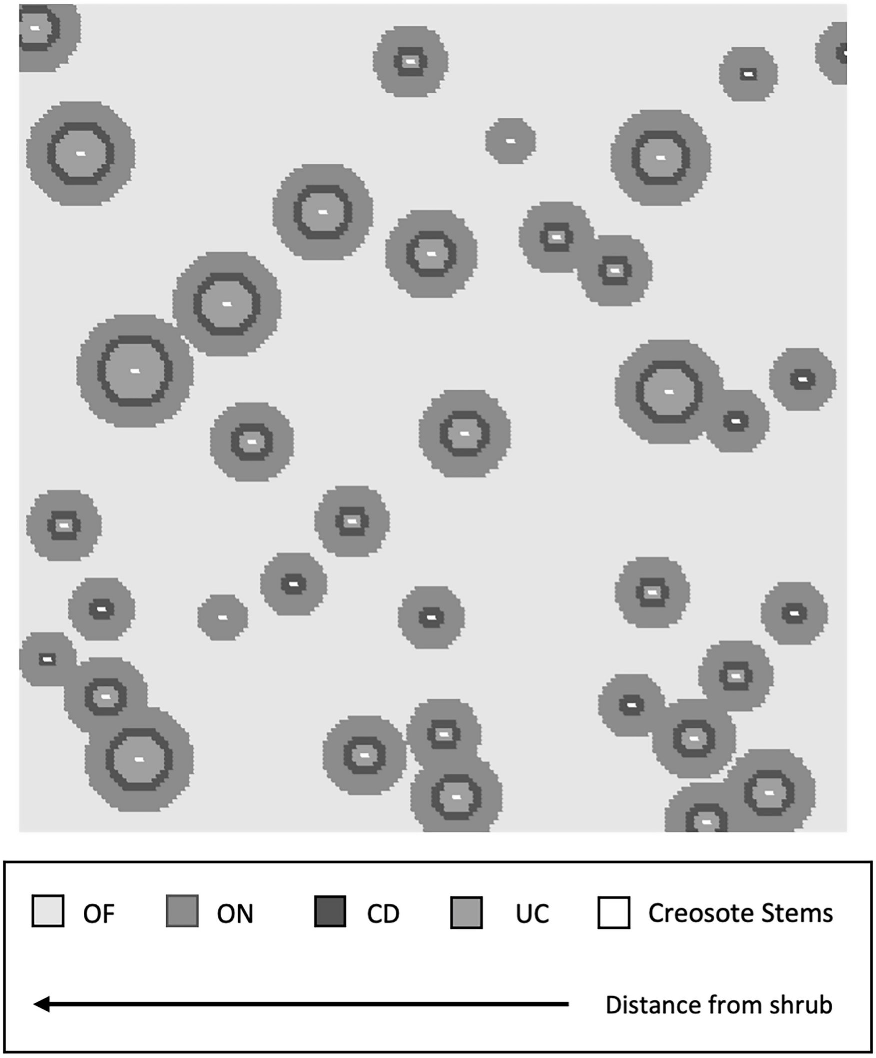

FIGURE 4 | Example of habitat zones in the Shrub Island model.

Probability of Spread Experiment [E-2]

In lowering *s* (the probability of fire spread from cell to cell) from a maximum value of 1.0 to a value of 0.5 (below the critical value) we see that the percolation probability curves shift to the right (**Figure 6**). This indicates that the number of cells that are capable of burning must increase to produce similar percolation probabilities as the cell-to-cell spread of fire decreases in probability. The curve with the probability of spread $s = 1.0$ in **Figure 6** is the same as the curve for the 400 × 200 cell landscape in **Figure 5**. Although the percolation curve for spread of 0.5 never reaches an upper value of 1.0 for any value of p_{cell}, there are by chance some cases where there is percolation as evidenced by values for the curve above 0.0.

Point-Spread Experiment [E-3]

When fires are initiated in a single location, the amount of the landscape that is impacted by fire can vary greatly among replicates with the same value of p_{cell} (**Figure 7**). In many cases, the proportion of flammable sites or total landscape burned can range from approximately zero to very high values. The highest values occur when all cells capable of burning are burned. The p_{crit} dividing line provides a good reference point to see how this works (**Figure 7**).

Proceeding from p_{cell} values of 0.55 (well below p_{crit}) to higher values, the maximum number of flammable sites burned among replicates increases, while many replicates still have a low proportion of sites burning, in many cases close to zero. The same trend is observed above p_{crit}, although the variance in proportion burned among replicates drastically decreases at p_{cell} values above approximately 0.65 (**Figure 7**). However, there are a few replicates that show a very low proportion of flammable sites and landscape burned for values of p_{cell} above 0.65 until a bit above 0.80. These low values of fire spread occur when the initial location set on fire falls in a rare neighborhood surrounded by sites that are not flammable.

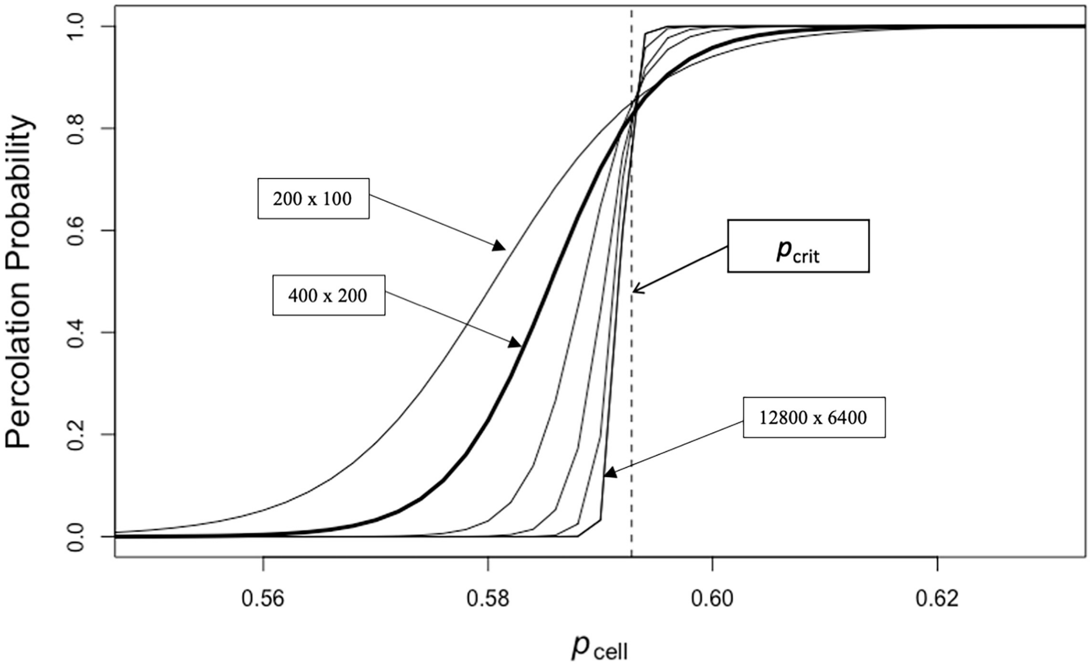

FIGURE 5 | Probability of fire percolation with landscapes of different size (Experiment E-1).

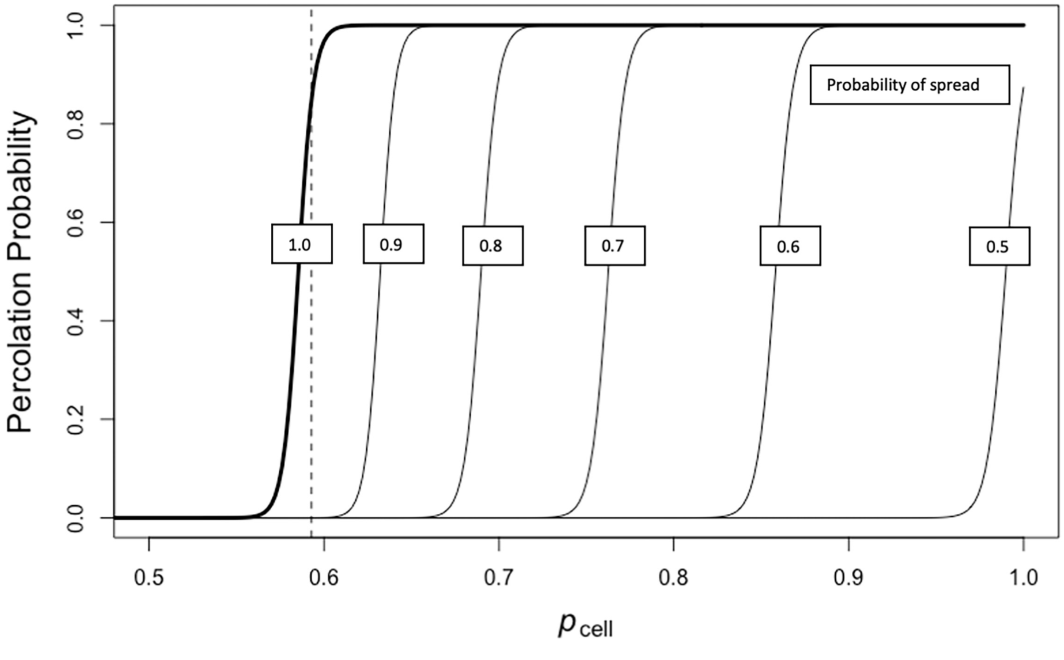

FIGURE 6 | Percolation probability of fire across a landscape with different probabilities of spread (s_{ij}) given varying levels of p_{cell} (Experiment E-2).

Shrub as Firebreak or Accelerant Experiment [E-4]

The impact of shrubs in the landscape changes the probability of percolation depending upon whether shrubs burn or don't burn (**Figure 8**). The direction of change in the percolation curve is as one would predict, with shrubs being able to burn shifting the percolation curve to the left (i.e., fire spreads easier at lower values of matrix flammability; low p_{cell} values). The curve shifts to the right when shrubs do not burn. These circumstances reflect changes that can occur with shifts in moisture status of creosote and annual plants protected from moisture loss by shading and the shrub-island effect under shrubs. Creosote branches and annuals with higher moisture content require higher levels of

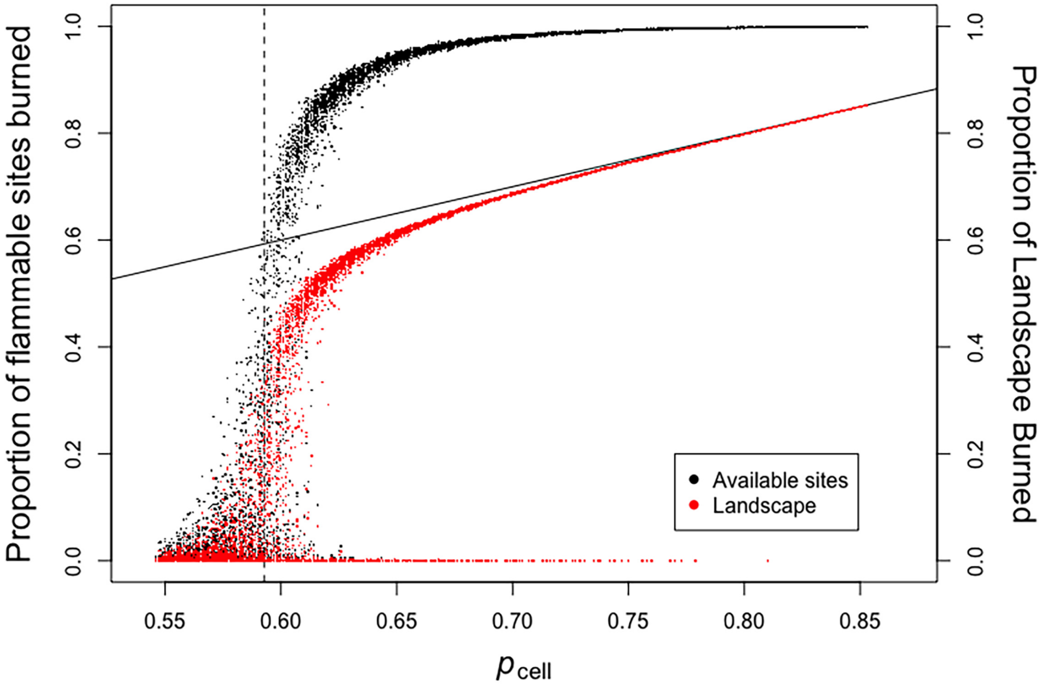

FIGURE 7 | Point source ignition experiments for a binary landscape. The probability of a cell being flammable (p_{cell}) was varied from 0.55 to 0.85 in increments of 0.002 for each burn experiment with 100 replicates for each value of p_{cell}. Proportion of available sites burned is the number of cells burned divided by the number of flammable cells in each model run. Proportion of landscape burned is the number of burned cells divided by the total number of model cells in each model run. The vertical dashed line is p_{crit}. The solid sloped line is $y = x$.

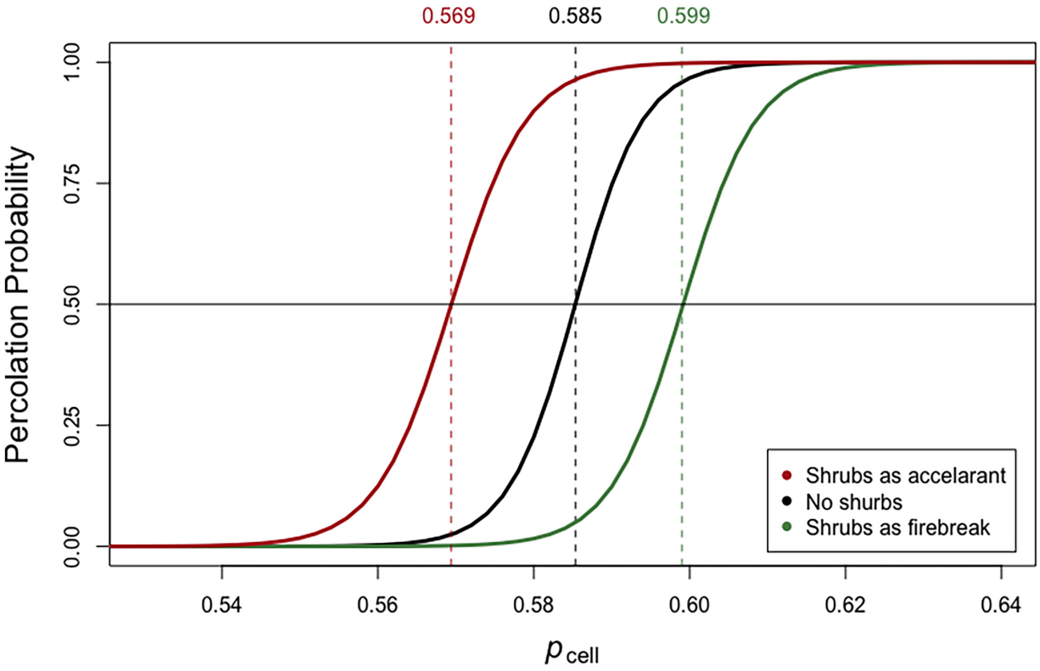

FIGURE 8 | Percolation probabilities for binary landscapes with shrubs acting as firebreaks (shrubs do not burn) or accelerants (shrubs burn) as compared to a landscape with no shrubs. Shrubs were randomly assigned with a distribution and size closely mimicking measured shrubs in the Mojave experiment (see section "Materials and Methods"). Vertical dotted lines are values at which there is a 50:50 probability that fire will percolate across the landscape in the vertical direction.

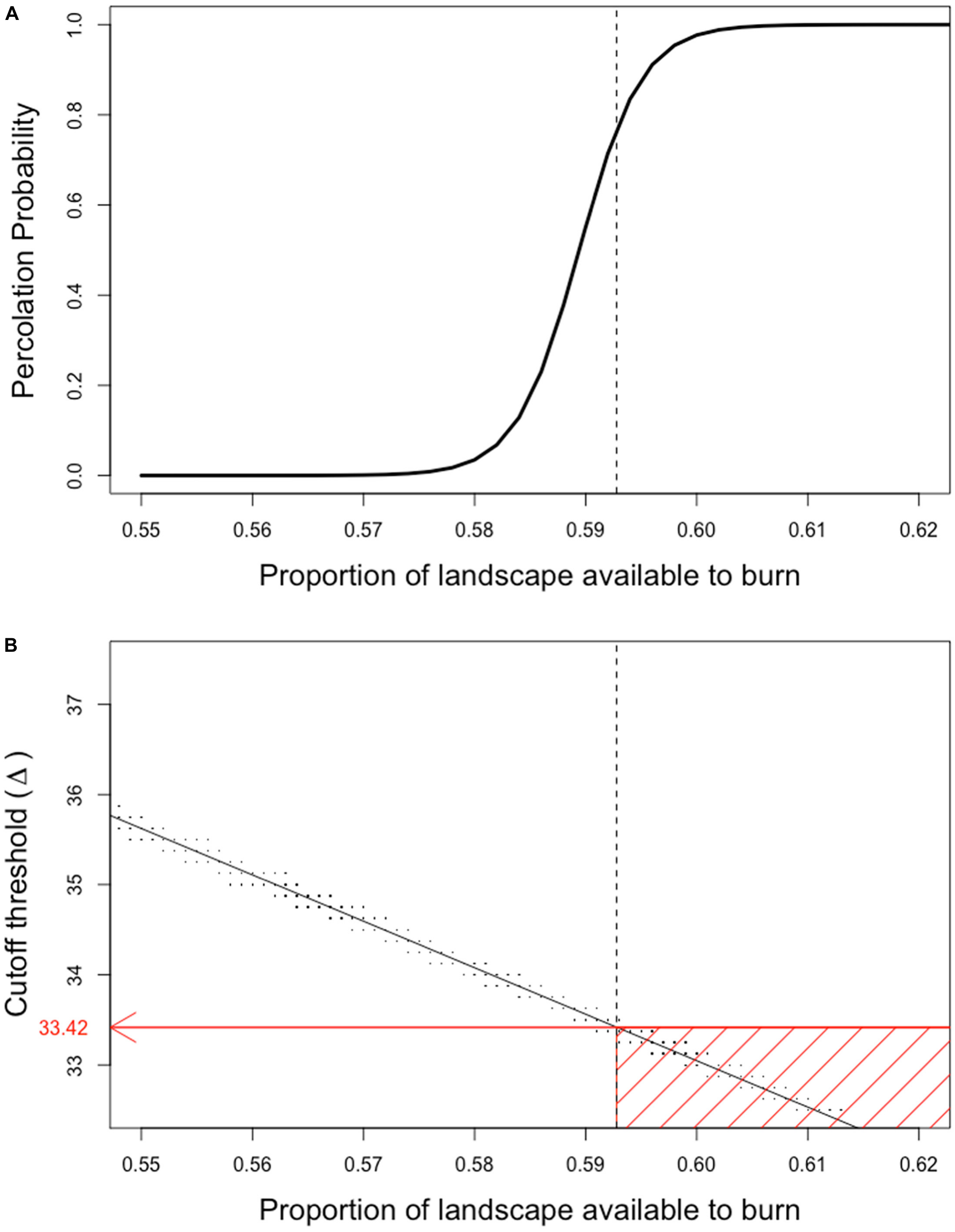

FIGURE 9 | Percolation probabilities and flammability of landscapes at different biomass thresholds of flammability. The proportion of landscape available to burn was the proportion of cells in the landscape that had biomass values at or above the flammability cutoff value Δ. All replicates had randomly assigned biomass distributions based on the biomass levels found under the high precipitation (E), no burn (UB) and no disturbance (UT) treatment in matrix (OF) treatment sites in the Mojave site experiment using a gamma distribution fit to field data (see section "Materials and Methods" and Moloney et al., 2019). **(A)** Shows the percolation probability at varying levels of landscape flammability (Proportion of landscape available to burn, effectively the p_{cell} value, was determined by calculating the proportion of cells with Δ or greater biomass, which were the cells that could spread fire). The solid line is the percolation probability curve fit to the observed model output. The dotted vertical line is at p_{crit}. **(B)** Shows the relationship between Δ and the proportion of the underlying landscape that is available to burn (effectively the p_{cell} value). Black dots represent the relationship between biomass cutoff values Δ and the underlying proportion of the landscape that is flammable at that cutoff value for replicate model runs. The dotted vertical line is at p_{crit}. The solid black line is the regression line of flammability threshold regressed on proportion of landscape available to burn. The horizontal red line is the biomass cutoff value that produces a landscape that has a proportion of burnable sites equal to p_{crit} determined by assessing the regression at a value of p_{crit}; this value can also be obtained directly from the probability density function associated with the gamma distribution used in producing the landscape (*cf*, the entry in **Table 2** for Mojave, 2013). The red box encompasses the range of conditions that will produce a landscape that will be guaranteed to percolate.

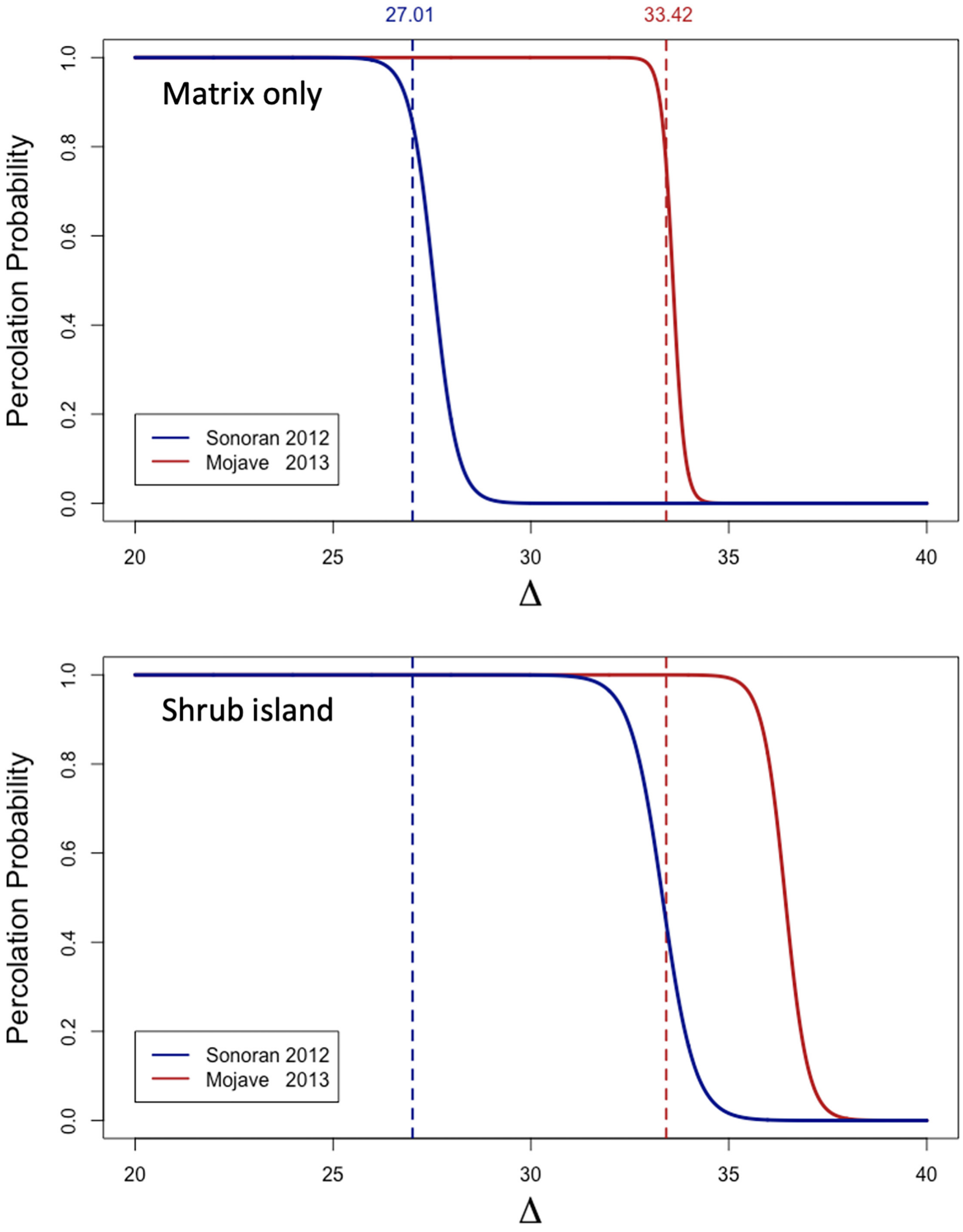

FIGURE 10 | Percolation probability as a function of biomass cutoff values (Δ) for high precipitation conditions during best growth years in Sonoran and Mojave Desert experiments, 2012 and 2013, respectively. Vertical dashed lines correspond to the biomass value that lies at p_{crit} as predicted from the gamma distribution for OF sites (**Table 3**). *Top panel:* These are the percolation probabilities for a model containing only matrix habitat based on the OF experimental plots for Sonoran and Mojave Desert Experiments. *Bottom panel*: These are the percolation probabilities for a shrub island model during the same year.

exposure to fires in the matrix and under the canopy to ignite (Fuentes-Ramirez et al., 2016).

Realistic Landscape Experiments

Biomass-Matrix Percolation Experiments [E-5]

Characterizing the matrix as being composed of annual plants with a gamma biomass distribution produces a percolation response similar to the response seen in the binary landscapes (cf., **Figure 9A** with **Figures 5**, **6**). As the proportion of the landscape that is flammable increases, we go from a landscape that doesn't percolate to one that always percolates once we have passed the critical threshold p_{crit}.

Although the percolation relationships for the current experiment and the binary landscape experiments are similar, the way we explore the relationship in the current experiment

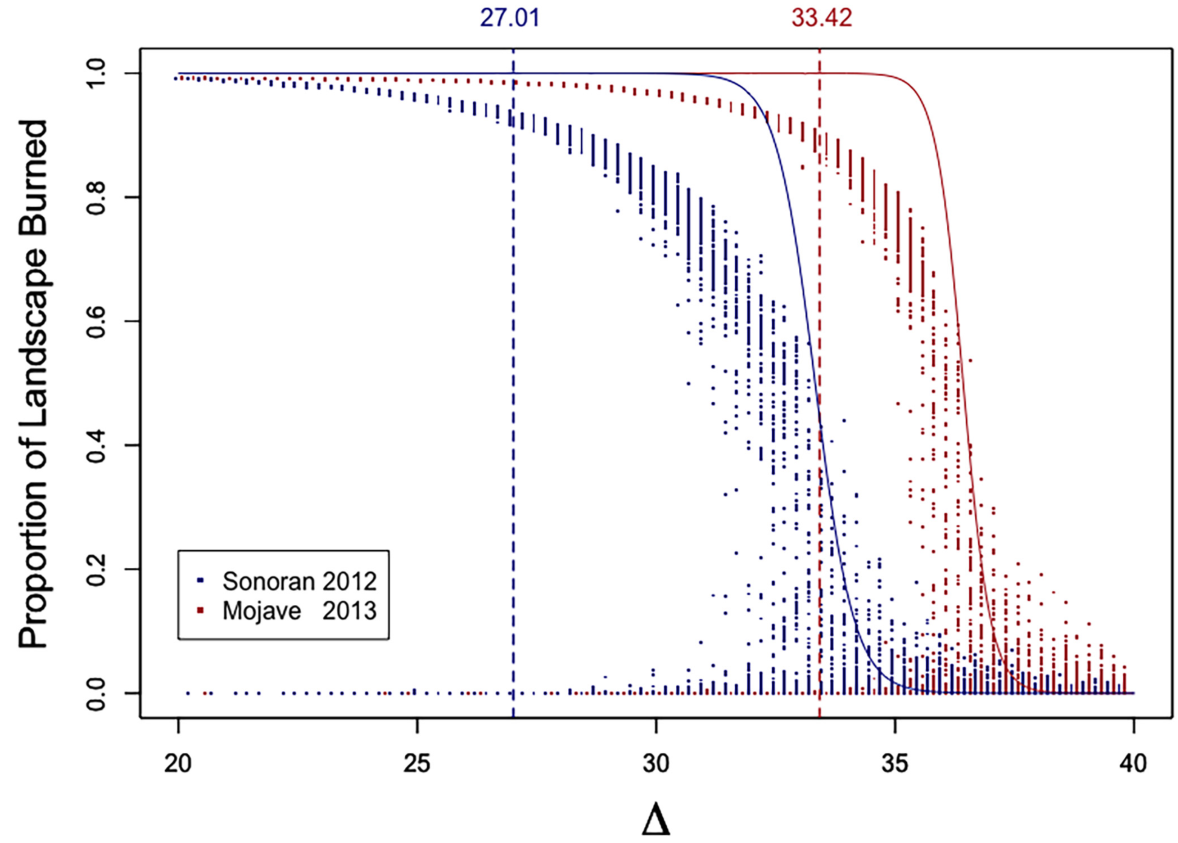

FIGURE 11 | Proportion of landscape burned by fire initiated within a single cell. Red points are replicates in the Mojave 2013 model and blue points in Sonoran 2012. Solid lines are the percolation probabilities shown in **Figure 10**. Vertical dashed lines correspond to the biomass value that lies at p_{crit} as predicted from the gamma distribution for OF sites (**Table 3**).

is fundamentally different. Here, the biomass distribution in the matrix is fixed by the values chosen for the gamma distribution determined from field measurements. Changes in fire spread are explored by changing the value of Δ, the biomass cutoff threshold, for a specific landscape (**Figure 9B**). As Δ values are lowered the proportion of the landscape that is available to burn increases, i.e., we are modeling conditions where it takes a lower amount of biomass to spread a fire when we lower the value of Δ. If we know the value of Δ from flammability experiments (e.g., Fuentes-Ramirez et al., 2016) we can then make predictions regarding the likelihood a fire will percolate across the landscape.

Using the gamma distribution, we can calculate the value of the biomass cutoff threshold Δ at which the landscape will be at the critical percolation threshold of p_{crit} (**Figure 9B**). With this as a benchmark, we can explore the percolation relationships as a function of Δ (**Figure 10**—upper panel). When we compare the 2013 Mojave and 2012 Sonoran model landscapes under increased precipitation (2× ambient rainfall), we find that there is a broader range of conditions in the Mojave landscape that will allow fire to percolate as compared to the Sonoran landscape. Basically, percolation in the Mojave will occur if fire spread occurs at standing biomass values of less than 33.42 g m^{-2}, whereas fire in the Sonoran will only percolate if it can spread at values less than 27.01 g m^{-2}. The implication is that the Mojave site would be more susceptible to fire spread than the Sonoran site, all things being equal. The relationships here however are quite artificial as they do not include the variability in biomass distributions produced by the shrub island effect, which were explored in the experiments discussed next.

Shrub-Island Experiments

Shrub-Island Percolation Experiment [E-6]

Comparing the shrub-island percolation experiment to the results for the biomass-matrix experiment (E-5), we see that the minimum biomass required to have a high probability for percolation shifts to higher values in the shrub-island model (**Figure 10**). The spread of fire is accelerated by the conditions associated with shrubs in the community. In examining **Table 3**, it is clear that this is due to the higher levels of biomass found in the microhabitats near to the shrubs (ON) and at the canopy dripline (CD). The effect is stronger for the Sonoran site model as can be seen in the larger shift to the right by the percolation curve for the shrub-island model (**Figure 10**). The increased shift may be due to the fact that the under-canopy microhabitat (UC) at the Sonoran site has biomass levels almost as high as the CD habitat, but in the Mojave they drop off markedly. The high level of fuel load continuity under shrubs in the Sonoran site act to accelerate fire spread more effectively than in the Mojave.

Shrub-Island Point-Spread Experiment [E-7]

As with the simple binary landscape, point-spread experiment [E-3], there is a great deal of variability in the amount of landscape burned after a point ignition over a range of biomass threshold (Δ) values (**Figure 11**). At even very low Δ values, there are instances where fire affects almost none of the landscape for both the Mojave and Sonoran models even though in most replicates a large proportion of the landscape burns. However, in general as Δ lowers there is less variability than at higher Δ values as the landscape becomes more interconnected and most flammable sites are reached by fire spread.

DISCUSSION

The sequence of model experiments presented here started with a very basic, binary landscape characterizing only two types of habitat, flammable and non-flammable, distributed at random. More "realistic" detail was then added to the model to explore the impact on the spread of fire of: (1) the differential likelihood of ignition of neighboring cells from a burning cell; (2) the presence of shrubs; and (3) patterns of biomass distribution based on field observations and precipitation experiments. By approaching the problem this way a deeper, more nuanced understanding of the process can be built up step-by-step. The alternative approach of building a more complete model and then exploring the dynamics is also a valid approach, but our view is that the latter approach is more appropriate for the study of specific systems and is not as generalizable.

Spread of Fire Across the Landscape (Percolation)

The experiments we used to explore the spread of fire across the landscape viewed fire spread through the lens of percolation theory, which has a fairly deep history in the modeling of fire and landscapes (Niessen and Blumen, 1986; Ohtsuki and Keyes, 1986; Grassberger, 2002; Zinck and Grimm, 2009; Abades et al., 2014). Percolation theory has also played a significant role in the discipline of landscape ecology in the development of an understanding of movement of organisms through fragmented landscapes, which can be viewed as analogous to the spread of fire; both fire and organisms require suitable habitat to move through the landscape (Wiens and Milne, 1989; Johnson et al., 1992; Wiens et al., 1997; Wu, 2013). Studying percolation of fire across a landscape element provides a macroecological view of the way fire can spread across the broader landscape.

As can be seen in our first model experiment [E-1], our understanding of the movement of fire across the landscape is influenced by the scale of the landscape considered. The likelihood that there will be a continuous path of flammable sites connecting across the landscape (percolating) shifts with changes in fuel availability. The smaller the landscape the more gradual the shift from a non-percolating landscape to a percolating landscape as the proportion of flammable sites increases (**Figure 5**). The reason for this is that larger landscapes will more likely have a random arrangement of sites that lead to a pathway of fuel from one edge of the landscape to another at a given probability of site flammability. This is due to what has been called the sampling effect (cf., Jarvis et al., 2017). Another factor affecting the likelihood that fire can percolate across the landscape is the likelihood that fire can spread from a burning site to adjacent sites in the neighborhood. Factors affecting this include fuel load, moisture status of vegetation, relative humidity, temperature, windspeed and wind direction (Benson et al., 2008; Fuentes-Ramirez et al., 2016; Estes et al., 2017). We explored the impact of changing conditions of spread in an experiment [E-2] altering the probability that a burning site will set an adjacent site with sufficient fuel to burn on fire (**Figure 6**). The impact of lower likelihood of spread, even with sufficient fuel, is to shift the curve representing the probability of spread across the landscape to higher levels of fuel load (i.e., p_{cell} in the binary landscape models) but it does not change the fundamental shape of the percolation response curve.

One could argue that the binary landscape models are too simplistic in their characterization of fire spread patterns. However, we have shown that adding more realism to the model by considering fuel loads in the form of biomass distributions [experiment E-5], rather than as a binary process, produces the same overall relationship as seen in the binary landscape model (i.e., percolation probabilities; **Figure 9**). The net effect of including biomass as a factor in fire spread is that it allows the ability to couple changes in fuel loads to shifts in probability of fire spread across the landscape within the modeling process.

The addition of shrubs as an accelerant or inhibitor of fire spread to the simple binary model [experiment E-4] does not change the fundamental relationships coupling fuel loads to spread across the landscape (**Figure 8**). We can view this simplistic depiction of the impact of shrubs as a proxy for the effect shrubs have on the fuel loads under their canopies. They act as an accelerant under conditions when shrubs lead to high fuel loads under their canopies, especially when conditions enhance flammability, e.g., low moisture conditions. In contrast, inhibition could be caused by low fuel loads under shrubs due to lower growth of annuals, low flammability due to higher moisture content or due to the qualities of the fuels themselves. Fuentes-Ramirez et al. (2016) have shown that some native annual species associated with under canopy habitat require hotter conditions and longer exposure to flames to ignite.

When shrubs were added to the model the rate of change in the probability of percolation from no-percolation to always percolate was not changed significantly. What does change is the position of the percolation curve with respect to the overall proportion of the matrix sites that are flammable (**Figure 8**). Shrubs acting as an accelerant shift the percolation probability curve toward lower values (i.e., fire percolates at lower fuel loads), whereas shrubs acting as an inhibitor (firebreak) shift the curve toward higher values. This is of course not surprising, but it does give some insights into the magnitude of that shift. The main benefit of these models is that they provide some insights into the range of conditions under which fire risk becomes enhanced. They can also be used to explore how changes in the distribution of shrubs might impact fire spread.

Spread of Fire From a Point Source

While the model experiments exploring the percolation process take a broad scale view, the experiments examining the spread of fire from random point-source ignitions examine the within landscape process of fire spread. An important component of this is the stochastic nature of fire spread due to the local pattern of site flammability in the neighborhood of the ignition point. In the binary landscape model [E-3], there is a rapid increase in the variability of fire spread among replicates as the proportion of flammable sites goes above 0.50 (**Figure 7**). This variability reflects the stochastic variability of neighborhood connectivity among flammable sites. Once the proportion of flammable sites surpasses about 0.62 the variability among replicates declines dramatically. Even so, until the proportion of flammable sites is above about 0.78 there are still replicates where fire spread is almost non-existence, i.e., the proportion of flammable sites and landscape burned is quite low in some replicates.

An examination of the "curve" for the proportion of landscape burned in **Figure 7** provides an insight into what occurs when the proportion of flammable sites is 0.75 or greater. Under these circumstances almost all (if not all) of the flammable sites are in contact with other flammable sites in their neighborhood. This is indicated by the fact that for a majority of replicates the number of sites burned is close to the number of flammable sites, i.e., the "proportion of landscape burned is approximately equal to p_{cell} on **Figure 7**. Under these circumstances the "proportion of flammable sites burned" approaches one. The few replicates that have a low proportion of sites burned represent rare instances where fire is initiated in a non-flammable cell or in a rare neighborhood where fire initiation occurs in a cell surrounded by a neighborhood of non-flammable sites.

Linking the More Realistic Biomass Model to the Binary Model

Shifting from the binary fire model to a more realistic approach requires a more nuanced definition of fire spread. Instead of a site being set as either flammable or non-flammable, sites are characterized by their fuel loads, i.e., standing biomass, based on field measurements of biomass distributions and their statistical properties. Modeling fire spread under these circumstances requires a consideration of both whether or not a cell can burn but also whether it contains enough biomass to spread fire to adjacent cells (cf., Fuentes-Ramirez et al., 2016). Basically, any cell containing measurable biomass can burn, but its ability to spread fire to neighboring cells depends upon the amount of biomass contained within the cell. With too little biomass, the fire in a cell is either not hot enough or of enough duration to ignite adjacent cells. Because of these considerations, the determinant of fire spread is the minimal biomass required to ignite adjacent cells on fire, i.e., the biomass cutoff threshold (Δ; **Table 1**). Setting a value for Δ in a model run determines the proportion of the landscape available to burn for the given biomass probability distribution, similar to choosing p_{cell} in the binary model. Any cell with Δ biomass or greater can spread fire. The equivalence between Δ and p_{cell} is shown in **Figure 9**.

The Shrub-Island Effect and Fire Spread

Our model experiments show that the impact of the shrub island effect during years of enhanced precipitation is to increase the extent of fire spread (**Figure 10**). This results from increased production of annual plants under creosote canopies. In contrast, fires that kill creosote lead to more open systems. One might assume that this could act to decrease the spread of fire due to diminishing the shrub island effect. However the impact of fire removing shrubs has other long term effects on the distribution of nutrients reducing the spatial concentration of N and K after the shrubs are killed (Fuentes-Ramirez et al., 2015b). Exotic annual grasses have also been shown to have enhanced competitive abilities relative to native annuals when soil nutrients are scarce (Brooks, 2000). The shift in nutrient distributions may consequently lead to an increase in fuel loads in the open and result in more frequent and intense fires in the future due to a more highly connected landscape (Brooks et al., 2004; Olsson et al., 2012). The current model could be adapted to consider these situations with a proper understanding of the distribution of biomass post-fire.

Implications for Fire Management

Our models show that a characterization of the probability distribution for biomass can be used to calculate the approximate value of the *Biomass threshold* Δ for matrix sites that will identify conditions producing a percolating landscape in the model (see **Tables 2**, **3**). If burn experiments indicate that the biomass required to produce ignition in adjacent locations is equal to the *Biomass threshold* or lower then there is a good chance that a fire can spread across the landscape. Under these conditions fire spread within the local landscape will also be extensive. The values that lead to fire spread can therefore be determined without the need to run simulation models once the parameters for the biomass probability distribution and required fuel load thresholds for spread are known.

The advantage of using Δ as a parameter to characterize the probability of fire spread is that it is a quantity that can be determined from burn experiments as in Fuentes-Ramirez et al. (2016). Once this is known, predictions regarding fire spread can be made from knowing biomass distributions in the field in conjunction with understanding the critical biomass threshold values under different conditions of hydration status. The impact of hydration on biomass can either be determined directly by harvesting standing biomass at a given site for years with different amounts of precipitation or by conducting simple irrigation experiments. One can even envision simple approximations of the effects of variable rainfall on fuel loads by comparing biomass among naturally variable patterns of water availability, e.g., washes vs. the bajada matrix. Obviously, such "space-for-time" analogs can only provide rough approximations and experimental approaches are expected to provide more accurate results (Damgaard, 2019).

It should be pointed out that the situations we have modeled probably represent conditions where fire will not spread extensively, since the conditions producing the greatest amount of biomass in our experiments yield a biomass threshold of approximately 33 g m^{-2} for the open (OF) matrix habitat (**Table 3**; Mojave-2013 High Precipitation Experiment). In contrast, published estimates of the threshold values for carrying fire in grass-dominated systems have been reported to be between 70 and 150 g m^{-2} (see Rao et al., 2015), at least double the maximum value we observed. The Rao et al.'s (2015) paper, which is a modeling study of fire size as a function of precipitation, N loading and biomass productivity in low-elevation desert scrub, found that there was no distinct biomass threshold that would produce extensive fires. However, they did find that the largest fires (99th percentile and above) were much bigger when winter fine-fuel production was above 125 g m^{-2}.

Given the biomass values we observed in our field experiment in the context of what is known about fuel loads necessary to carry fire, there is no potential for extensive fire spread under the conditions occurring at the time of our study, even with an addition of 2× ambient precipitation. Our experiments were conducted during a time of historic drought in the Desert Southwest. However, model predications for the Southwestern US suggest that, although the area will become generally hotter and drier (Cayan et al., 2010; Woodhouse et al., 2010), the area also may be impacted by more extreme rainfall events (Diffenbaugh et al., 2005; Wang and Zhang, 2008). It remains to be seen whether or not extreme rainfall events, coupled with continued invasion by annual grasses, will increase fuel loads to the extent that the potential for extensive fires becomes a concern. Applying our modeling approach may, however, have benefits if applied to desert grassland systems that already have higher fuel loads due to local environmental conditions. The models may also be used to predict when the systems we studied will be at greater risk of catastrophic fire spread either through an increase in invasive species biomass in the open or through extreme rainfall events.

Future Explorations

The model described here is a work in progress and could be adapted to include more elements that might increase the ability to more accurately predict rates and patterns of fire spread in desert shrublands. A short list of the possibilities include: (1) more realistic spatial patterns of biomass distribution perhaps coupled to models of water movement in the landscape; (2) a nuanced understanding of the flammabilities of different plant species that may be associated with different habitat zones; (3) addition of the effects of shrubs that burn and lead to the spread of fire by windblown embers and belowground spread of fire by roots; and (4) inclusion of plant demography in response to fire and moisture over time. Each of these elements would allow the development of a more nuanced understanding of fire in these systems and with enough work could lead to models coupled with models of climate to look at long term trends.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KM designed and conducted the field experiments used to parameterize the model, wrote the model code, parameterized, conducted, and analyzed the model experiments. KM, CH, and AF-R contributed to writing the manuscript. CH designed and conducted the field experiments used to parameterize the model. AF-R was responsible for developing the conceptual three component igniter-spreader-shrub model of fire spread that informed the development of the simulation models presented here. All authors contributed to the article and approved the submitted version.

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REFERENCES

Abades, S. R., Gaxiola, A., Marquet, P. A., and Sala, O. (2014). Fire, percolation thresholds and the savanna forest transition: a neutral model approach. *J. Ecol.* 102, 1386–1393. doi: 10.1111/1365-2745.12321

Abella, S. R. (2009). Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. *J. Arid Environ.* 73, 699–707. doi: 10.1016/j.jaridenv.2009.03.003

Allen, E. B., Steers, R. J., and Dickens, S. J. (2011). Impacts of fire and invasive species on desert soil ecology. *Rangeland Ecol. Manage.* 64, 450–462. doi: 10.2111/rem-d-09-00159.1

Amoroso, L., and Miller, D. M. (2006). *NTC Soils. Surgical Geologic Map of Arid Southwestern USA*. Washington, DC: U.S. Geological Survey.

Baddeley, A., Rubak, E., and Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications With R*. Boca Raton, FL: CRC.

Benson, R. P., Roads, J. O., and Weise, D. R. (2008). "Chapter 2 climatic and weather factors affecting fire occurrence and behavior," in *Developments in Environmental Science*, eds A. Bytnerowicz, M. J. Arbaugh, A. R. Riebau, and C. Andersen (Amsterdam: Elsevier), 37–59. doi: 10.1016/s1474-8177(08)00002-8

Bolker, B. M. (2008). *Ecological Models and Data in R*. Princeton, NJ: Princeton University Press.

boost.org (2014). *Boost C++ Libraries*.

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., et al. (2009). Fire in the earth system. *Science* 324, 481–484.

Bradley, B. A., Curtis, C. A., and Chambers, J. C. (2016). "Bromus response to climate and projected changes with climate change," in *Exotic Brome Grasses in Arid and Semiarid Ecosystems of the Western US*, eds C. Brown, J. Chambers, and M. Germino (Berlin: Springer).

Brooks, M. L. (2000). Competition between alien annual grasses and native annual plants in the Mojave Desert. *Am. Midland Nat.* 144, 92–108. doi: 10.1674/0003-0031(2000)144[0092:cbaaga]2.0.co;2

Brooks, M. L. (2002). Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecol. Appl.* 12, 1088–1102. doi: 10.1890/1051-0761(2002)012[1088:pftaeo]2.0.co;2

Brooks, M. L., and Matchett, J. R. (2006). Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *J. Arid Environ.* 67, 148–164. doi: 10.1016/j.jaridenv.2006.09.027

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., et al. (2004). Effects of invasive alien plants on fire regimes. *BioScience* 54, 677–688. doi: 10.1641/0006-3568(2004)054[0677:eoiapo]2.0.co;2

Cary, G. J. (2002). *Importance of a Changing Climate for Fire Regimes in Australia. Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. Cambridge: Cambridge University Press, 26–46.

Cayan, D. R., Das, T., Pierce, D. W., Barnett, T. P., Tyree, M., and Gershunov, A. (2010). Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proc. Natl. Acad. Sci. U.S.A.* 107, 21271–21276. doi: 10.1073/pnas.0912391107

Chambers, J. C., and Wisdom, M. J. (2009). Priority research and management issues for the imperiled great basin of the western United States. *Restor. Ecol.* 17, 707–714. doi: 10.1111/j.1526-100x.2009.00588.x

Charley, J. L., and West, N. E. (1975). Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *J. Ecol.* 63, 945–963. doi: 10.2307/2258613

Chen, J., Shiyomi, M., Hori, Y., and Yamamura, Y. (2008). Frequency distribution models for spatial patterns of vegetation abundance. *Ecol. Model.* 211, 403–410. doi: 10.1016/j.ecolmodel.2007.09.017

Cox, J. T., and Durrett, R. (1988). Limit theorems for the spread of epidemics and forest fires. *Stoch. Process. Appl.* 30, 171–191. doi: 10.1016/0304-4149(88)90083-x

Damgaard, C. (2019). A critique of the space-for-time substitution practice in community ecology. *Trends Ecol. Evol.* 34, 416–421. doi: 10.1016/j.tree.2019.01.013

D'Antonio, C. M., and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87. doi: 10.1146/annurev.es.23.110192.000431

Diffenbaugh, N. S., Pal, J. S., Trapp, R. J., and Giorgi, F. (2005). Fine-scale processes regulate the response of extreme events to global climate change. *Proc. Natl. Acad. Sci. U.S.A.* 102, 15774–15778. doi: 10.1073/pnas.0506042102

Engel, E. C., and Abella, S. R. (2011). Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *J. Appl. Ecol.* 48, 1401–1410. doi: 10.1111/j.1365-2664.2011.02057.x

Esque, T. C., Webb, R. H., Wallace, C. S. A., van Riper, C., McCreedy, C., and Smythe, L. (2013). Desert fires fueled by native annual forbs: effects of fire on communities of plants and birds in the lower Sonoran Desert of Arizona. *Southwest. Nat.* 58, 223–233. doi: 10.1894/0038-4909-58.2.223

Estes, B. L., Knapp, E. E., Skinner, C. N., Miller, J. D., and Preisler, H. K. (2017). Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA. *Ecosphere* 8:e01794. doi: 10.1002/ecs2.1794

Ewing, S. A., Southard, R. J., Macalady, J. L., Hartshorn, A. S., and Johnson, M. J. (2007). Soil microbial fingerprints, carbon, and nitrogen in a Mojave Desert creosote-bush ecosystem. *Soil Sci. Soc. Am. J.* 71, 469–475. doi: 10.2136/sssaj2005.0283

Fuentes-Ramirez, A., Mudrak, E. L., Caragea, P. C., Holzapfel, C., and Moloney, K. A. (2015a). Assessing the impact of fire on the spatial distribution of *Larrea tridentata* in the Sonoran Desert, USA. *Oecologia* 178, 473–484. doi: 10.1007/s00442-014-3214-1

Fuentes-Ramirez, A., Schafer, J. L., Mudrak, E. L., Schat, M., Parag, H. A., Holzapfel, C., et al. (2015b). Spatio-temporal impacts of fire on soil nutrient availability in *Larrea tridentata* shrublands of the Mojave Desert, USA. *Geoderma* 259-260, 126–133. doi: 10.1016/j.geoderma.2015.05.016

Fuentes-Ramirez, A., Veldman, J. W., Holzapfel, C., and Moloney, K. A. (2016). Spreaders, igniters, and burning shrubs: plant flammability explains novel fire dynamics in grass-invaded deserts. *Ecol. Appl.* 26, 2311–2322. doi: 10.1002/eap.1371

Garcia-Moya, E., and McKell, C. M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51, 81–88. doi: 10.2307/1933601

Gardner, R. H., Milne, B. T., Turnei, M. G., and O'Neill, R. V. (1987). Neutral models for the analysis of broad-scale landscape pattern. *Landsc. Ecol.* 1, 19–28. doi: 10.1007/bf02275262

Grassberger, P. (2002). Critical behaviour of the Drossel-Schwabl forest fire model. *New J. Phys.* 4, 17–17. doi: 10.1088/1367-2630/4/1/317

Grissino Mayer, H. D., and Swetnam, T. W. (2000). Century scale climate forcing of fire regimes in the American Southwest. *Holocene* 10, 213–220. doi: 10.1191/095968300668451235

Jarvis, N., Larsbo, M., and Koestel, J. (2017). Connectivity and percolation of structural pore networks in a cultivated silt loam soil quantified by X-ray tomography. *Geoderma* 287, 71–79. doi: 10.1016/j.geoderma.2016.06.026

Johnson, A. R., Milne, B. T., and Wiens, J. A. (1992). Diffusion in fractcal landscapes: simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73, 1968–1983. doi: 10.2307/1941448

Marlon, J. R., Bartlein, P. J., Carcaillet, C., Gavin, D. G., Harrison, S. P., Higuera, P. E., et al. (2008). Climate and human influences on global biomass burning over the past two millennia. *Nat. Geosci.* 1, 697–702. doi: 10.1038/ngeo313

Moloney, K. A., Mudrak, E. L., Fuentes-Ramirez, A., Parag, H., Schat, M., and Holzapfel, C. (2019). Increased fire risk in Mojave and Sonoran shrublands due to exotic species and extreme rainfall events. *Ecosphere* 10:e02592. doi: 10.1002/ecs2.2592

Mudrak, E. L., Moloney, K. A., Fuentes-Ramirez, A., Schafer, J. L., Haines, C. E., and Holzapfel, C. (2011). "Spatial patterns in the distribution of creosote (*Larrea tridentata*) and burrobush (*Ambrosia dumosa*) in the Mojave and Sonoran deserts: a template for fire risk," in *Proceeding of the 96th Annual Ecological Society of America Meeting*, (Austin, TX).

Mudrak, E. L., Schafer, J. L., Fuentes-Ramirez, A., Holzapfel, C., and Moloney, K. A. (2014). Predictive modeling of spatial patterns of soil nutrients related to fertility islands. *Landsc. Ecol.* 29, 491–505. doi: 10.1007/s10980-013-9979-5

Niessen, W. V., and Blumen, A. (1986). Dynamics of forest fires as a directed percolation model. *J. Phys. A* 19:L289.

Ohtsuki, T., and Keyes, T. (1986). Biased percolation: forest fires with wind. *J. Phys. A* 19:L281.

Olsson, A. D., Betancourt, J., McClaran, M. P., and Marsh, S. E. (2012). Sonoran desert ecosystem transformation by a C4 grass without the grass/fire cycle. *Divers. Distrib.* 18, 10–21. doi: 10.1111/j.1472-4642.2011.00825.x

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Randerson, J. T., Chen, Y., van der Werf, G. R., Rogers, B. M., and Morton, D. C. (2012). Global burned area and biomass burning emissions from small fires. *J. Geophys. Res.* 117:G04012.

Rao, L. E., Matchett, J. R., Brooks, M. L., Johnson, R. F., Minnich, R. A., and Allen, E. B. (2015). Relationships between annual plant productivity, nitrogen deposition and fire size in low-elevation California desert scrub. *Int. J. Wildland Fire* 24, 48–58. doi: 10.1071/wf13152

Schafer, J., Mudrak, E., Haines, C., Parag, H., Moloney, K., and Holzapfel, C. (2012). The association of native and non-native annual plants with Larrea tridentata (creosote bush) in the Mojave and Sonoran Deserts. *J. Arid Environ.* 87, 129–135. doi: 10.1016/j.jaridenv.2012.07.013

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., and Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374. doi: 10.2307/2265615

Sugihara, N. G., van Wagtendonk, J. W., and Fites-Kaufman, J. (2006). "Fire as an ecological process," in *Fire in California's Ecosystems*, eds N. G. Sugihara, J. W. van Wagtendonk, J. Fites-Kaufman, K. E. Shaffer, and A. E. Thode

(Berkeley, CA: University of California Press), 58–74. doi: 10.1525/california/9780520246058.003.0004

Thompson, D. B., Walker, L. R., Landau, F. H., and Stark, L. R. (2005). The influence of elevation, shrub species, and biological soil crust on fertile islands in the Mojave Desert, USA. *J. Arid Environ.* 61, 609–629. doi: 10.1016/j.jaridenv.2004.09.013

Vasek, F. C. (1980). Creosote bush: long-lived clones in the Mojave Desert. *Am. J. Bot.* 67, 246–255. doi: 10.2307/2442649

Wang, J., and Zhang, X. (2008). Downscaling and projection of winter extreme daily precipitation over North America. *J. Clim.* 21, 923–937. doi: 10.1175/2007jcli1671.1

Wang, Z., Chappellaz, J., Park, K., and Mak, J. E. (2010). Large variations in southern hemisphere biomass burning during the last 650 years. *Science* 330, 1663–1666. doi: 10.1126/science.1197257

Whelan, R. J. (1995). *The Ecology of Fire*. Cambridge: Cambridge University Press.

Wiens, J. A., and Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landsc. Ecol.* 3, 87–96. doi: 10.1007/bf00131172

Wiens, J. A., Schooley, R. L., and Weeks, R. D. (1997). Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78, 257–264. doi: 10.2307/3546292

Woodhouse, C. A., Meko, D. M., MacDonald, G. M., Stahle, D. W., and Cook, E. R. (2010). A 1,200-year perspective of 21st century drought in southwestern North America. *Proc. Natl. Acad. Sci. U.S.A.* 107, 21283–21288. doi: 10.1073/pnas.0911197107

Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. *Landsc. Ecol.* 28, 1–11. doi: 10.1007/s10980-012-9836-y

Zinck, R. D., and Grimm, V. (2009). Unifying wildfire models from ecology and statistical physics. *Am. Nat.* 174, E170–E185.

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Grassification and Fast-Evolving Fire Connectivity and Risk in the Sonoran Desert, United States

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In the southwestern United States, non-native grass invasions have increased wildfire occurrence in deserts and the likelihood of fire spread to and from other biomes with disparate fire regimes. The elevational transition between desertscrub and montane grasslands, woodlands, and forests generally occurs at ∼1,200 masl and has experienced fast suburbanization and an expanding wildland-urban interface (WUI). In summer 2020, the Bighorn Fire in the Santa Catalina Mountains burned 486 km^2 and prompted alerts and evacuations along a 40-km stretch of WUI below 1,200 masl on the outskirts of Tucson, Arizona, a metropolitan area of >1M people. To better understand the changing nature of the WUI here and elsewhere in the region, we took a multidimensional and timely approach to assess fire dynamics along the Desertscrub-Semi-desert Grassland ecotone in the Catalina foothills, which is in various stages of non-native grass invasion. The Bighorn Fire was principally a forest fire driven by a long-history of fire suppression, accumulation of fine fuels following a wet winter and spring, and two decades of hotter droughts, culminating in the hottest and second driest summer in the 125-yr Tucson weather record. Saguaro (*Carnegia gigantea*), a giant columnar cactus, experienced high mortality. Resprouting by several desert shrub species may confer some post-fire resiliency in desertscrub. Buffelgrass and other non-native species played a minor role in carrying the fire due to the patchiness of infestation at the upper edge of the Desertscrub biome. Coupled state-and-transition fire-spread simulation models suggest a marked increase in both burned area and fire frequency if buffelgrass patches continue to expand and coalesce at the Desertscrub/Semi-desert Grassland interface. A survey of area residents six months after the fire showed awareness of buffelgrass was significantly higher among residents that were evacuated or lost recreation access, with higher awareness of fire risk, saguaro loss and declining property values, in that order. Sustained and timely efforts to document and assess fast-evolving fire connectivity due to grass invasions, and social awareness and perceptions, are needed to understand and motivate mitigation of an increasingly fire-prone future in the region.

Keywords: grass-fire cycle, wildland-urban interface, invasive species, El Niño southern oscillation (enso), invasive species management, Sonoran Desert, desert shrublands

INTRODUCTION

The frequency and size of large fires across western North America are increasing with longer growing and fire seasons, record high temperatures, and more severe and hotter droughts, specifically since the mid-1980s (Abatzoglou and Williams, 2016; Westerling, 2016). An equally important driver are non-native grass invasions that have altered wildfire regimes at mid to low elevations in semi-arid areas (Fusco et al., 2019).

Desert shrublands, characterized mostly by long-lived shrubs (and cacti in the subtropics) and extensive areas of barren soil, dominate the lowest elevations (<1,200 masl) in the region. These shrublands expanded with warming and drying during the Holocene, with many species reaching their northernmost distributions only during the past few millennia (e.g., McAuliffe and Van Devender, 1998; Koehler et al., 2005; Holmgren et al., 2007). Although historical evidence is lacking, conventional wisdom has it that the wide spacing of plants and insufficient continuity of fuel renders these desert shrublands mostly fireproof, specifically in the hot subtropical deserts (Mojave, Sonoran, and Chihuahuan), which harbor mostly non-fire adapted taxa. A contributing factor to the prevalence of barren ground may be the recency of desert shrublands and a lengthy delay in the migration and establishment of perennial plants that can take advantage of the underutilized space and resources (Betancourt, 2012). The prevalence of barren soil, however, may be due in large part to seasonal aridity and insufficient soil moisture. After infrequent wet (El Niño) winters, much of the empty space between shrubs and cacti fills with native annual forbs that decompose rapidly and do not greatly affect fuel loads (Brooks, 1999). In recent times, desert fires were confined to these wet years when there was sufficient fine fuel to carry a wildland fire, most frequently in June when the fuels had dried out (McLaughlin and Bowers, 1982).

Evidence for the lack of frequent or extensive wildfires in Sonoran and Mojave Desert desertscrub vegetation prior to grass invasions is mostly indirect but still persuasive. Neither foothill palo verde (*Parkinsonia micophylla*) nor the giant columnar cactus (*Carnegiea gigantea*), the dominant species in the Arizona Upland of the Sonoran Desert, are fire resistant. Saguaro has long-lived but fire-sensitive epidermis and foothill palo verde has photosynthetic bark that can be damaged easily by fire; individuals of both are seldom consumed by fire but they are often killed by girdling or top-killed. Saguaros do not resprout. Foothill palo verdes can resprout after fire, but re-sprouting plants are susceptible to repeated fires. Recruitment of both foothill palo verde and saguaro is slow. Evidence for the lack of fire historically includes regional surges in saguaro regeneration between 1780 and 1860 throughout southern Arizona, long prior to 20th-century grass invasions and altered fire regimes (Pierson et al., 2013).

Red brome (*Bromus rubens*), a non-native annual grass that fuels desert fires, spread rapidly into the Mojave and Sonoran Deserts with frequent consecutive wet winters associated with the positive phase of the Pacific Decadal Oscillation (PDO) from 1977 to 1995 (Salo, 2005). Wildfires in the Arizona Upland of the Sonoran Desert increased in frequency beginning in the 1970s (McLaughlin and Bowers, 1982; Rogers, 1986; Schmid and Rogers, 1988) and tapered off with increasing aridity between 1999 and 2004 (Alford et al., 2005). That changed dramatically following the wet El Niño winter of 2004–2005, when an unprecedented ∼5,000 km^2 burned in desertscrub across the Mojave and Sonoran Desert (Brooks et al., 2013). Invasive-fueled fires tend to die out in uninvaded desertscrub, much like wildfires in semi-desert native grassland, woodlands, and forests at higher elevations invariably die out downslope as they also encounter uninvaded desertscrub (see Brooks and Pyke, 2001; Parker, 2002). It remains an untested though likely assumption that wildfires were uncommon and of limited spatial extent prior to the introduction and spread of non-native grasses.

The notion of fireproof deserts has changed in recent decades with the exponential spread of both winter annual (e.g., cheatgrass: *Bromus tectorum,* Spanish and red brome: *B. madritensis* and *B. rubens,* Mediterranean grass: *Schismus barbatus*) and perennial C$_4$, (buffelgrass: *Cenchrus ciliaris*, fountain grass: *C. setaceus*, Lehmann's lovegrass: *Eragrostis lehmanniana*) non-native grasses capable of colonizing the copious bare areas available in desert shrublands. The result of these grass invasions has been a large increase in the frequency and size of wildfires at desert elevations (Schmid and Rogers, 1988; Alford et al., 2005). This is a self-perpetuating grass-fire cycle that progressively excludes native plants and results in grassification, the physiognomic conversion of shrublands to grassland (D'Antonio and Vitousek, 1992; Williams and Baruch, 2000; Brooks and Chambers, 2011; Betancourt, 2015).

A new fire mosaic is being established in the region whereby wildfires driven by invasive grasses can spread from the desert valleys to the forested mountains, and vice versa (**Figure 1**). Fire-adapted vegetation communities occur on the "Sky Islands" (mountains) of the southwestern U.S. and northwest Mexico in a classic elevational zonation gradient from Semi-desert Grasslands to oak and chaparral, up to mixed conifer forests (Merriam, 1890; Whittaker and Niering, 1965). Fire regimes in mountains of western North America have been altered over the last century or more. Livestock grazing and fire suppression have resulted in fuel buildup over the last 150 years, culminating in more frequent large forest fires, with record warming and drying in recent decades exacerbating the trend (Westerling, 2016). Meanwhile, non-native grass invasions and novel fire regimes in desert shrublands and increased urbanization at lower elevations in recent decades are transforming fire dynamics at the wildland-urban interface (WUI) of the Sky Islands, where the deserts meet the forests.

The socioeconomic impacts of these novel wildfire regimes are considerable and mounting. Much of the physical infrastructure and urban development in the arid parts of the western United States is concentrated at desert elevations, in precisely those areas most affected by grass invasions and associated fire risks. Population density and mobility facilitate both the spread of non-native grasses and human ignitions. Managers of public lands, transportation departments, and cities and towns now need to plan around a novel and fast-evolving fire risk, and they face escalating non-native plant (fuels) control and fire suppression costs at a time when federal, state, and local government budgets are being flatlined and are not keeping up with inflation and increasing need. Other economic costs include decreased property values and a reevaluation of fire insurance in increasingly fire-prone areas, as well as losses in tourism revenue with decaying ecological backdrops.

The impacts of grass invasions and associated wildfires are not limited to desert elevations. In the 21st century, the largest desert wildfires have burned 10^4–10^5 ha, with some spreading from the basins to the mountains, altering fire regimes in adjacent native grasslands, chaparral, woodlands, and forests. The spread of broad ignition fronts from grass-invaded desert shrublands to forested highlands, and vice versa, is probably novel. This new fire dynamic has yet to be addressed specifically in the scientific literature about grass invasions, altered wildfire regimes, and management of the WUI that characterizes mountain piedmonts in the western United States. Notable wildfires that were fueled in large part by red brome and other non-native winter annuals in summer 2005 at desert elevations, and burned across the WUI into adjacent vegetation types, include the Cave Creek Complex Fire (1,005 km^2) in Central Arizona, the Southern Nevada Complex Fire (2,059 km^2), and the Hackberry Fire (236 km^2) in eastern California. These wildfires were preceded by an unusually wet El Niño year and a broadly synchronous bloom of red brome and other non-native winter annuals. These large fires heralded what one writer called "The Year We Lost the Desert" (Clark, 2006). After another wet winter in 2019–2020, the Bush Fire (783 km^2) was fueled by red brome and Mediterranean grass on the outskirts of Phoenix in central Arizona and burned upslope into the Superstition Mountains. Further south, the Bighorn Fire (486 km^2) burned over much of the Santa Catalina Mountains on the outskirts of Tucson, Arizona, a metropolitan area supporting more than a million people. The 2020 Bighorn Fire provided us the opportunity to evaluate the spread of an ignition front at the Desertscrub/Semi-desert Grassland ecotone, which is in various stages of buffelgrass and other grass invasions in the Catalina Foothills.

To better understand the changing nature of the WUI in the region, we assessed the impacts of the 2020 Bighorn Fire in desertscrub weeks to months after it happened. Our aims were to: (1) establish a baseline of expansion and infestation of buffelgrass in the Santa Catalina Foothills WUI; (2) evaluate the fire behavior and the degree to which fire spread or died out in Desertscrub invaded (or not) by buffelgrass; (3) quantify species responses to the fire, including losses of the iconic saguaro; (4) adapt a state-and-transition fire-spread model to simulate present and future fire risks associated with buffelgrass invasion; and (5) assess whether the fire affected residents' perceptions of buffelgrass as a fire threat. We use this case study to draw broader lessons about grass invasions and altered wildfire regimes in the North American subtropics and elsewhere.

MATERIALS AND METHODS

Study Area

The Tucson Basin, encompassing the Tucson Metropolitan Area in southern Arizona, spans an area of 1,200 km^2 and is bounded by mountain ranges including the Tucson Mountains to the West and the Santa Catalina (Catalinas herein), Rincon, and Santa Rita Mountains to the north, east, and south, respectively. The Catalinas form part of the Coronado National Forest, established in 1908. The elevational gradient is steep, rising from ∼800 masl in the City of Tucson on the basin floor to ∼2,800 masl on Mt. Lemmon, the highest peak in the Catalinas, a distance of just 30 km. Temperature and precipitation gradients are accordingly sharp. Average annual temperature and precipitation is 20°C and 300 mm in Tucson and 10°C and 750 mm on Mt. Lemmon. These contrasts are reflected in vegetation zonation of the Catalinas, which spans seven different biomes: Arizona Upland Sonoran Desertscrub, Semi-desert Grassland, Oak Woodland, Chaparral, Oak-pine Woodland, Ponderosa Pine Forest, and Mixed Conifer Forest (e.g., Whittaker and Niering, 1965; Brusca and Moore, 2013; **Figure 1**). The Desertscrub biome occupies elevations below 1,200 masl and contains plant communities characterized by dense stands of foothill palo verde and saguaro, highly diverse and in various stages of invasion by non-native grasses. Directly above Desertscrub is Semi-desert Grassland, an open grassland with scattered woody species spanning 1,200 to 1,400 masl but extending to 1,700 masl on xeric slopes. Dominated by summer-flowering annual and perennial grasses, grass cover can increase by 50% after wildfires, which are frequent, mostly natural, and generally die out at Desertscrub's edge (Whittaker and Lowe, 1984).

The most prominent and aggressive invasive grass species in the Sonoran Deserts is buffelgrass (*Cenchrus ciliaris,* syn. *Pennisetum ciliare*), a flammable grass native to Africa, the Middle East, and southern Asia and invasive in subtropical areas of Australia, North America, South America, and many islands in the Pacific Ocean (including Hawaii), Indian Ocean and the Caribbean Sea. In North America, buffelgrass was introduced to improve cattle yields (State of Sonora, Mexico) and control erosion (Arizona) beginning in the 1930s. By the 1980s, buffelgrass was spreading rapidly throughout Arizona with landscape level expansion in Sonora, Mexico (e.g., Franklin et al., 2006). In the Sonoran Desert, buffelgrass reduces species richness and diversity of native vegetation through competition

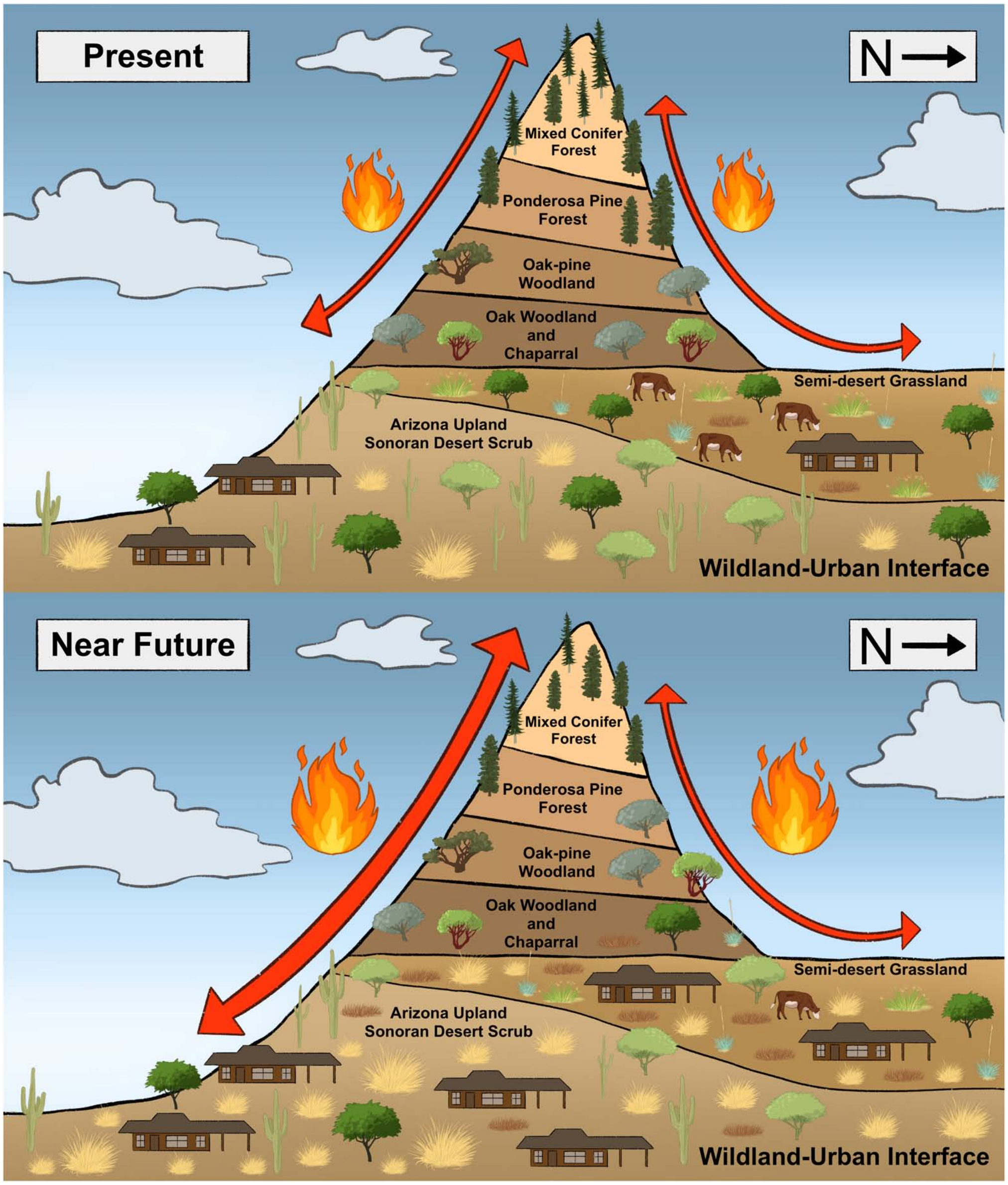

FIGURE 1 | Conceptual representation of grassification driven fire connectivity of the Sky Islands of arid North America. Present conditions have an expanding front of non-native grasses that will promote an increase of fuels and connectivity at the wildland-urban interface and the Desertscrub/Semi-desert Grassland ecotone in the coming years and couple decades (Figure by MRS).

(Olsson et al., 2012a) and elevates fire risk at the WUI (Olsson et al., 2012b). Buffelgrass burns hotter than most other native and non-native grasses, reaching fire temperatures of 800–900°C (McDonald and McPherson, 2013). Measured buffelgrass fuel loads range from 250 to 900 g/m^2 at study sites in Southern Arizona, more than sufficient to drive grassland fire (Esque et al., 2007; McDonald and McPherson, 2013). Buffelgrass fuel loads fluctuate less than that of non-native, winter annual grasses, creating a more consistent fire hazard in the arid foresummer (May-June).

The forest fire history of the Catalinas during the past four centuries is relatively well known thanks to fire scar studies using tree rings (Iniguez et al., 2008, 2016). It is characterized by frequent and episodic surface fires that decreased dramatically at the turn of the 20th century due to prolonged livestock grazing and fire suppression. Increasing fuel loads and connectivity eventually led to major wildfires: the 2002 Bullock Fire (124 km^2), the 2003 Aspen Fire (344 km^2), and the 2020 Bighorn Fire (486 km^2). In addition, in the summer of 2019 the Mercer Fire (0.1 km^2) was ignited by lightning in a dense saguaro-palo verde stand heavily infested with buffelgrass.

The Bighorn Fire was started by a lightning strike late on June 5, 2020, in steep and rugged terrain of the Pusch Ridge Wilderness area in the southwest corner of the Catalinas, overlooking the fast-growing suburban town of Oro Valley on the northern outskirts of Tucson (**Figures 2**, **3**). By July 23, when the fire was 100% contained, the largest recorded wildfire in the Catalina Mountains had burned 486 km^2, pushed by a delayed and dry monsoon season, periodic strong winds, and the hottest summer in Tucson's 125-yr weather record. These hot and dry conditions were preceded by a wet winter 2019 and early spring 2020, which added fine fuels in desertscrub from abundant winter annuals, including the invasive red brome.

The fire ignited on a steep, north-facing slope on the southwestern flanks of the Catalinas at ∼ 1,200 masl. The fire moved from west to east into the Catalina front range and, on the nights of June 11, 20, and 21, dropped down into canyons at the edge of the WUI and forced alerts and evacuations of homes in the desert near the Coronado National Forest boundary (**Figure 2**). At the same time, the fire pushed north and by June 11^{th} had grown to more than 25 km^2, threatening nearly 1,000 homes in the municipality of Oro Valley

FIGURE 2 | The Santa Catalina Mountains and 2020 Bighorn Fire, Tucson, Arizona. Counter clockwise from top: Looking north over the of City of Tucson to the Catalina Mountains from Tumamoc Hill, photo by Paul Mirocha; front range of the Catalinas with buffelgrass infested south-facing slopes (yellow patches inside white circles), photo courtesy of the Arizona-Sonora Desert Museum; The Bighorn Fire dropping down the front range of the Catalinas into Ventana Canyon and the Tucson wildland-urban interface, 20 June 2020, photo by A.T. Willett; slurry bomber dropping retardant just above the WUI on the front range of the Catalinas, 12 June 2020, photo by BTW.

and the Catalina Foothills community of Tucson. The fire later threatened the mountain village of Summerhaven, which was successfully defended by firefighters. The fire also threatened the town of Oracle on the north flank, and ranches to the east, before eventually dying out as humidity increased with a late onset of the monsoon.

Between August and December 2020, several of the authors undertook day hikes to locations along the lower edge of the Bighorn Fire (**Supplementary Figure 1**). The goals were (1) to assess the fuels that brought the fire to its lowest extent, especially the role of native and non-native species, including buffelgrass and (2) assess the landscape features that halted the fire. In some cases, it was impossible to identify the burned remains, but frequently we could identify species by re-sprouting stems. To aid identification, we also extrapolated from unburned islands of vegetation, often smaller than a meter square, spared by firebreaks created by natural features such as exposed rock formations.

Mapping Buffelgrass Infestation

Buffelgrass has been steadily expanding in the Catalina foothills, or the front (south) range of the Catalina Mountains adjacent to

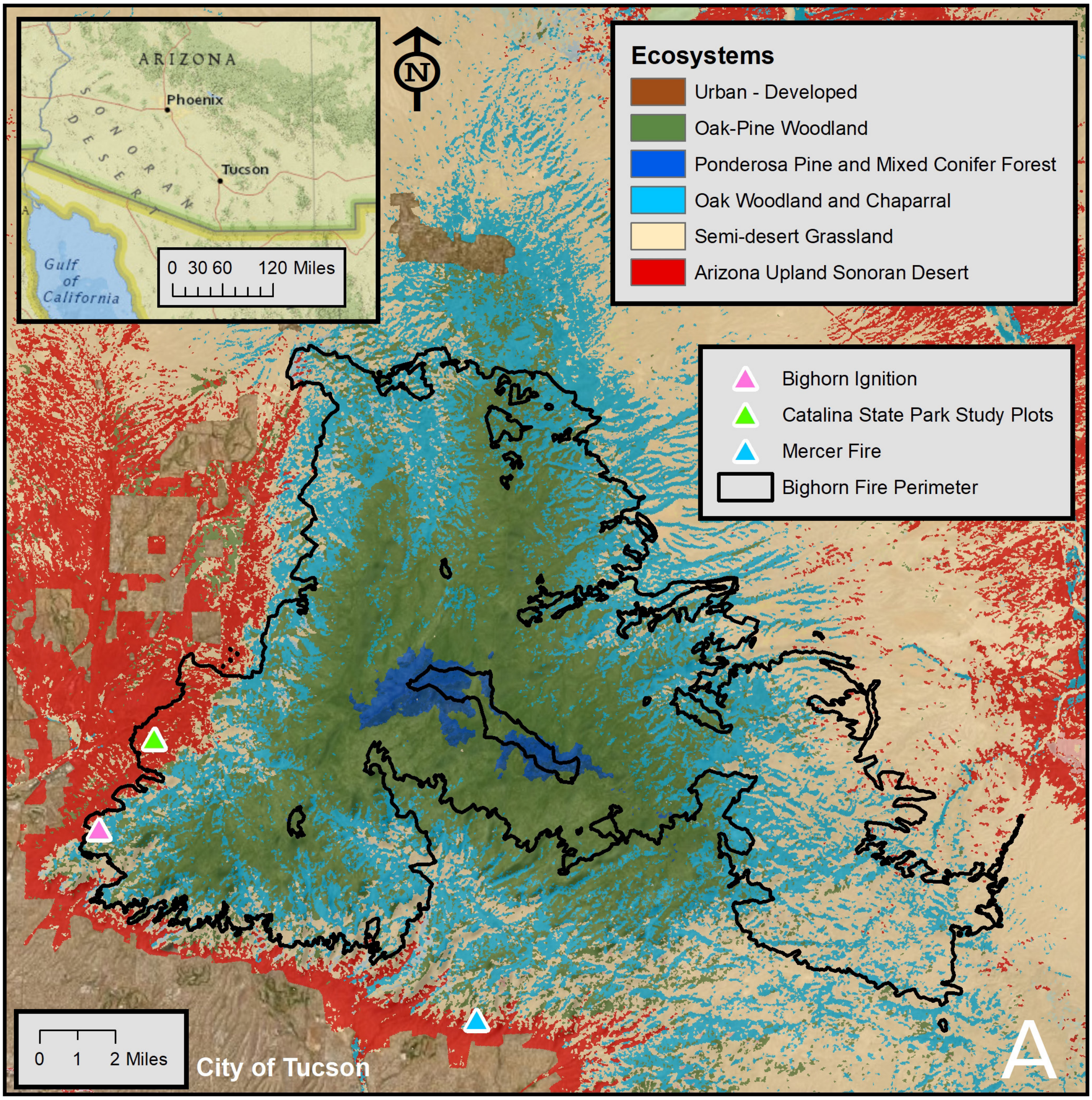

FIGURE 3 | *(Continued)*

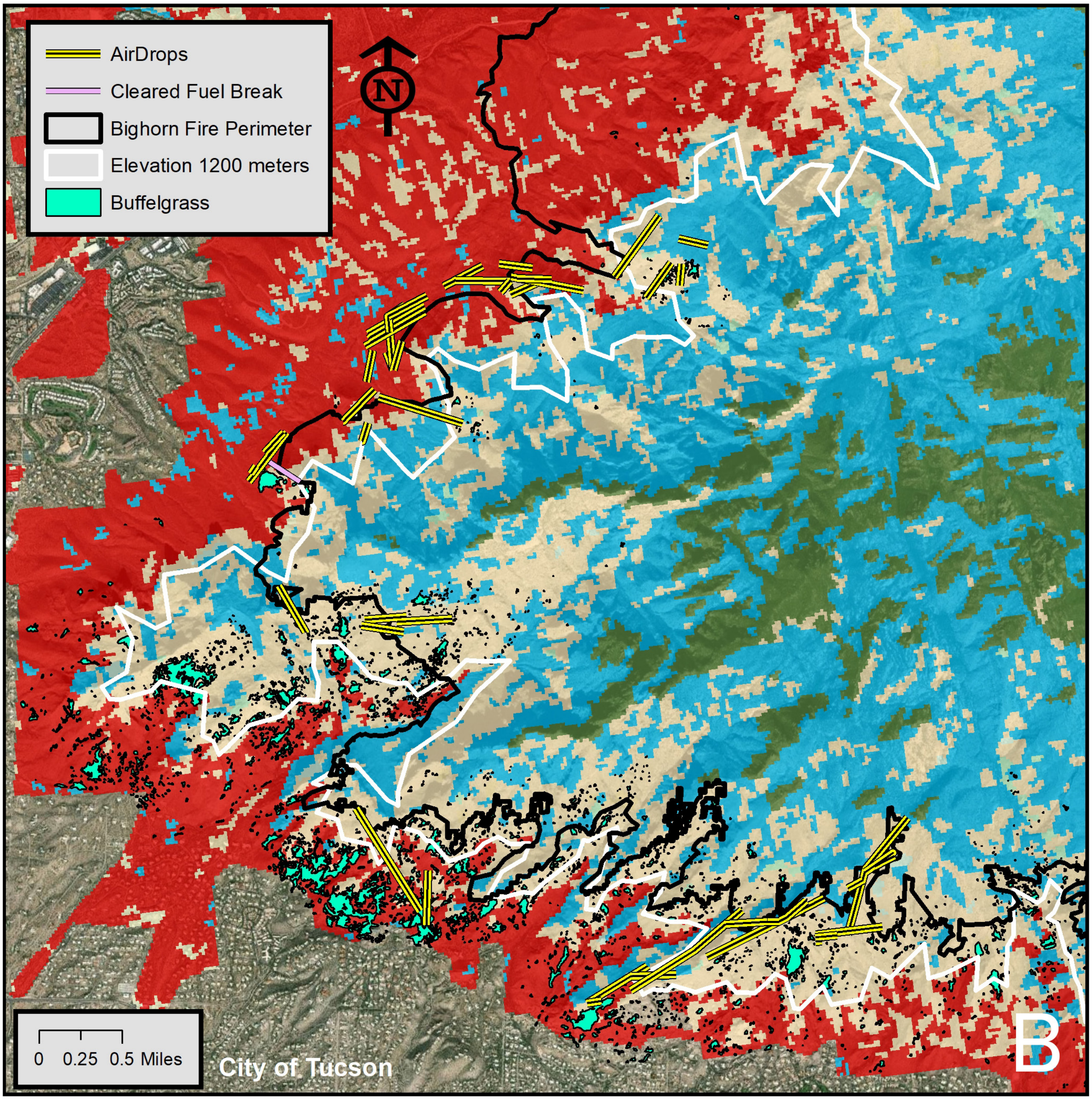

FIGURE 3 | The Santa Catalina Mountains and the Bighorn Fire perimeter. **(A)** The Catalina Mountains and ecosystems. **(B)** Close up of the southwest portion of the Catalina Mountains and the wildland-urban interface with present-day buffelgrass infestation, Bighorn Fire suppression efforts, and the 1,200 masl Desertscrub/Semi-desert Grassland ecotone.

Tucson for several decades (**Figures 2**, **3B**). Previous attempts to map the infestation in time and space were made in 2008 and 2016 but quality of accuracy and precision, and even positive identification, have been questioned by stakeholders. This has limited an understanding of rates of spread, treatment efforts, fire prevention or other management actions.

We used Google Earth Pro, historical aerial photography, and satellite imagery to map the buffelgrass distribution in 2018 as a close estimate of the extent of the infestation at the time of the 2020 Bighorn Fire. The entire front range of the Catalinas was scanned from 1,500 masl to the WUI. Polygons were drawn around buffelgrass patches seen on the best historical imagery. A "patch" is defined as a mostly contiguous area of buffelgrass plants or a distinct cluster of buffelgrass plants amid an area of non-buffelgrass. The assessment of whether or not a feature was identified as buffelgrass was based on expert opinion rooted in field experience and observations. Experience with remote sensing of buffelgrass via a variety of techniques and image types for effective mapping (Olsson et al., 2009, 2011; Elkind et al., 2019) led to the decision that, for this particular area, hand-drawn aerial photo interpretation was more accurate than existing surveys and automated techniques using multispectral imagery.

Identifying and mapping buffelgrass in the Catalinas is possible because of the unique growth pattern that makes it a threat in wildfire-based ecosystem transformation. The high cover of homogenous buffelgrass cover in invaded areas differs distinctly from the rich and diverse structure of nearby uninvaded areas that are dominated by bare mineral soil but boast high species and structural diversity. In a study of buffelgrass impacts on species diversity that includes portions of the Catalinas affected by the fire, Olsson et al. (2012b) found the interiors of buffelgrass patches to be characterized by $>44\%$ buffelgrass cover with very little species diversity. These characteristics make aerial photo interpretation of buffelgrass boundaries both practical and effective as demonstrated by Olsson et al. (2012b) and validated by Olsson and Morisette (2014).

Given the variable nature of the imagery, the topographical layout of the Catalinas, and the relative abundance of different imagery due to proximity to a high-value imaging target (Tucson), image quality varied across the region. As such, some areas were mapped with higher confidence than others. South and southwest-facing imagery, which have good lighting properties in satellite images, are good habitat for buffelgrass. In these areas buffelgrass patches tend to be dense and have discrete boundaries that decrease in size with distance from a central focal point (possibly the original infestation location). This pattern is easier to positively identify than patches in which buffelgrass is diffuse or scattered evenly among other vegetation. Smaller patches are harder to distinguish and confidently assess because there are fewer visual cues that convey the texture or color of a buffelgrass patch. They tend to be easier to map more confidently when larger patches are nearby because color and texture are easier to compare and spatial autocorrelation indicates that a small patch is more likely to be found next to a big patch than all by itself on an otherwise clear hillslope.

North- and north-east facing slopes tend to have higher vegetation density of native vegetation. Above 1,200 masl, Arizona Upland Sonoran Desertscrub transitions into Semi-desert Grassland and buffelgrass is found in both ecosystems, though it decreases in occurrence as elevation increases. Buffelgrass is less distinct when situated in a matrix of native and other non-native grasses of the higher-elevation desert grassland.

The accuracy of the map has been estimated by ground truthing in select areas in combination with fuel assessment hikes (see "Study area" above and **Supplementary Figure 1**) of the Catalina front range. Systematic statistical methods for accuracy assessment of the map have not been performed yet due to time and budget constraints. Visual comparisons of the map with previous helicopter-based surveys conducted by the USFS in 2008 and 2016 indicated dramatic improvement in accuracy and precision (**Supplementary Figure 2**). From a statistical perspective, in 2008, 210 polygons were mapped covering 787.25 acres (an average of 3.75 acres). In 2016, a largely disjoint set of 206 polygons were mapped covering 906.02 acres (an average of 4.4 acres per polygon). In contrast, this hand-digitized effort mapped 162 acres with 2068 polygons, an average of 0.08 acres per polygon.

Quantification of Species Responses to Fire

Saguaros

To understand the impact of fire on saguaro mortality in the Catalina Mountains, sampling plots were established in the footprint of the Mercer Fire. On August 22, 2019, a lightning strike ignited and burned 0.1 km^2 of a south-facing slope of Arizona Upland Sonoran Desertscrub heavily infested with buffelgrass before running out of fuel (buffelgrass) and dying out. Ten sampling plots 20 m × 20 m in size in the fire area were established in November 2020, and five plots of the same size in the adjacent non-burned area (**Figure 3**). The four corners of each plot were permanently marked with rebar.

Any standing saguaros within a plot were labeled with a uniquely numbered aluminum tag. For each saguaro within a plot, we recorded whether it was dead or alive. A saguaro was considered dead if it had fallen or was completely devoid of chlorophyll (green photosynthetic skin). We measured each saguaro's height, the range of skin (epidermis) injured by the fire, the number of established arms, the number of developing arms (nubs), and the phenology of the cactus (experiencing active growth, flowering, bearing fruits, or bearing remains of flowers or fruits). Fire-caused skin injury includes charred skin, which usually appeared at the base of a burned saguaro, as well as burn scars with a light tan color devoid of chlorophyll. Active growth of a saguaro was indicated by the presence of white, soft spines on the newest areoles of the cactus.

Data were analyzed using a linear mixed model to determine any linear relationship between the height of a saguaro and the amount of plant tissue damaged (percent of skin burned) by the Mercer Fire. Individual plots were treated as a random effect in the model and only a random intercept was evaluated. The regression was performed using the lmer function in the "lme4" package in the R environment (Bates et al., 2015). We compared the log-likelihood of this model with a null model with the same random effect to determine the significance of this relationship.

We predicted the future mortality of each saguaro based on the amount of burn damage per plant through reconstructing the relationship between mortality and burned area following Esque et al. (2004). In that study, the authors acquired a nonlinear relationship between the fire scorch range recorded one month after the 1994 Mother's Day Fire in Saguaro National Park and the mortality of saguaros six years after the fire. We estimated the approximate values of both variables from their published figure and fitted them with a general additive model. We then used this model to predict the future mortality of saguaros surveyed at the Mercer Fire site.

Vegetation Plots

To understand the impact of the Bighorn Fire on desert vegetation and future recovery and community composition, twenty permanent 15 m × 15 m vegetation monitoring plots were established at Catalina State Park, Tucson, Arizona (**Figure 3**). These were divided equally between two vegetation types: Arizona Upland Sonoran Desertscrub, and Semi-desert Grassland. Within each vegetation type, five plots were established in an area burned in the Bighorn Fire, and five control plots were established outside of the burn area.

Within each plot, species richness and abundance of perennial species were recorded. Individuals were categorized as dead or alive, and in the burned plots, we counted the number of living individuals with post-fire regrowth or resprouting. For annual species, presence was recorded, but abundance and regrowth status were not. Cover estimates for each species were obtained along three parallel, 15 m long transect-intercept lines within each plot. Dead and living tissue were recorded separately, and in the burned plots, living tissue was categorized as either post-fire regrowth or unburned living tissue. Dried winter annuals from the previous season were not identifiable to species and thus were grouped. Likewise, all perennial grass species (native and non-native) in both the burned and unburned treatments could not be confidently identified to species and were labeled to "perennial grass" for most analyses. Data were taken in November, due to extremely low summer monsoon precipitation of 2020, sprouting and growth of live plants was greatly reduced.

State-and-Transition Fire-Spread Models

We used existing datasets, models, and tools, as well as recent research from the area, in a state-and-transition modeling approach to produce the most accurate set of potential outcomes from a large, complex wildfire in the short time frame that would be most useful to managers. Spatially explicit state-and-transition simulation models (STSM) can simulate landscape dynamics to evaluate complex and often uncertain future conditions (Daniel et al., 2016), including forecasting plant invasions (Frid and Wilmshurst, 2009; Frid et al., 2013; Grechi et al., 2014; Jarnevich et al., 2015). These models divide a landscape into discrete spatial units (cells) that are assigned a discrete state. While STSM can simulate some fire dynamics, these are based on parameterization from historical fires. We have dynamically linked an STSM to a fire model based on physical characteristics to overcome knowledge limitations that would otherwise prevent parameterization of the novel invasive species-driven fires (Jarnevich et al., 2019). As the simulation runs, changes to states over discrete time steps are tracked by the model and these states are passed to the fire model that then simulates fire on the landscape. The fire model provides information on which cells burned, indicating where fire transition should occur in the STSM. Transitions between states can be probabilistic or time-based and are specific to transition type (e.g., growth, treatment, disturbance, etc.). The STSM model used for this study was adapted from a STSM model developed for nearby Saguaro National Park (**Supplementary Figure 3**; Jarnevich et al., 2019, 2020). We merged this model with components of an earlier simulation for the Catalina Mountain study area (**Supplementary Figure 4**; 14,216 km^2).

The model divides the landscape into seven states: uninvaded, buffelgrass seedbank, and one of five buffelgrass cover class levels [$<$1%, 1–10%, 11–0%, $>$50%, converted ($>$50% cover that has burned)] and allows movement between states including dispersal, establishment, patch infilling (increase in buffelgrass cover class), and fire. The uninvaded states are further split into fuel models. To implement the simulations, we used the stsim base package (version 3.1.21) with the stsim-farsite add-on package (version 3.1.21) within the SyncroSim version 2.0.41 software. The stsim-farsite package integrates the FARSITE fire area simulator software version 4.1.055 into ST-Sim (Finney, 2004).

A LANDFIRE fuel model classification of the study area (Landfire, 2020) defined fuel model classes across the landscape to simulate wildfire. Increasing numbers of fuel models added to the complexity of the STSM and thus to computational requirements. Fuel models with very small pixel counts were combined with other similar fuel model classes, and we noted the potential differences caused by the changes (**Supplementary Table 1**). We also modified fuel models for northern aspects (NW-N-NE) for three random timesteps to reflect the frequency of years preceded by two "wet" winters, which create an increase in annual grass fuel loads on these aspects (see Rogers and Vint, 1987). These fuel models formed the basis for scenarios that did not include buffelgrass on the landscape.

For buffelgrass scenarios, additional inputs to simulations included the initial distribution of buffelgrass in the front range of the Catalinas (from section "Mapping buffelgrass infestation"), and a previously developed habitat suitability map for buffelgrass classifying the landscape into areas susceptible or unsusceptible to buffelgrass invasion (Frid et al., 2013). For cells with buffelgrass, the fuel model was defined based on fuel levels for buffelgrass invaded areas of different cover amounts following Jarnevich et al. (2019). Previous work defined 10% buffelgrass cover as required to carry a fire (or 0.5 ton/acre of fuel, estimated based on McDonald and McPherson, 2013). Thus, all landscape states could be cross walked to a fuel model. Transition parameter values followed Saguaro National Park simulations with patch infill transitions to a higher buffelgrass cover class state based on the moderate rates of patch infill and its interaction with precipitation (Jarnevich et al., 2019, 2020).

For the FARSITE parameters (**Supplementary Table 2**), we incorporated most of the values used by fire modelers contemporaneously working on the Bighorn Fire in the Wildland Fire Decision Support System (Noonan-Wright et al., 2011). Because their fire duration value was based on estimates related to operational questions rather than ecological conditions, we used the mean fire duration of historic wildfires in adjacent Saguaro National Park to identify the fire duration. This value of 45 days better matched the period of active fire growth of the Bighorn Fire, and simulation results without buffelgrass matched the historic fire size frequency of the Santa Catalina Mountains. Fire history for the study area (1932–2009) shows 8.6 fires over 100 ha in size over 30 years; more recent data (2000–2019) calculates to 12 per 30 years. We also modified the fire season start and end days based on expert opinion from local fire ecologists/wildland fuels specialists. This process used established data, models and tools supplemented by current research and expert opinion to inform the most accurate potential outcomes in a rapid time frame.

Surveying Resident Perceptions

To understand the impact of the fire on area residents' perceptions of buffelgrass as a fire risk, we surveyed a sample of

Pima county residents, randomly selected but weighted to ensure representation of people living in the Catalina foothills area near the Bighorn Fire. The sample was collected via Qualtrics, a third-party marketing firm. The survey was answered by 2,147 respondents, which resulted in a final sample of 550 complete responses, pseudo response rate of 25.62%. The final sample excluded 1,113 respondents who either overfilled demographic quotas (14.11%) or did not reside in our sample area (37.73%). Other respondents were also excluded due to failed attention checks (3.03%), speeding (3.35%), or not fully completing the questionnaire (16.16%). Data collection took place in January and February of 2021. Respondents were asked whether they had heard of buffelgrass before (yes/no/maybe), and if so to rate their awareness (Likert scale from 1–10) of several buffelgrass threats (i.e., increased risk of fire, loss of saguaro cactus, and declining property values). The survey also asked whether respondents had been affected by the fire, with response options that included evacuation; evacuation of family or friends; and loss of recreational access to the Catalina Mountains. The questionnaire featured additional questions regarding a choice experiment of a hypothetical bond package for invasive species control not covered here that are the focus of ongoing research.

RESULTS

Fire Behavior

The Bighorn Fire was ignited on a north slope below Bighorn Peak at about 1,200 masl among native Semi-desert Grassland species including sotol (*Dasilyrion wheeleri*), beargrass (*Nolina microcarpa*), bullgrass (*Muhlenbergia* sp.), buckwheat (*Eriogonum wrightii*), rosewood (*Vaquelinia californica*), and occasional mulberry (*Morus micropylla*) and scrub oak (*Quercus turbinella*). All were observed to be resprouting post-fire.

The fire backed down a steep north-facing slope into vegetation transitional to the Arizona Upland of the Sonoran Desert. Species in this area are mostly sotol, ocotillo (*Fouquieria splendens*), mesquite (*Prosopis velutina*), club moss (*Selaginella spp.*), prickly pear (*Opuntia spp.*), and hopbush (*Dodonaea viscosa*). Bunchgrasses were common, including native bush muhly (*Muhlenbergia porteri*), sideoats grama (*Bouteloua curtipendula*), purple three-awn (*Aristida purpurea*) and spider grass (*A. ternipes*) as well as non-native weeping lovegrass (*Eragrostis curvula*) and Lehmann's lovegrass. The primary fuels, however, were expired winter annuals, especially native mustards (Brassicaceae), forget-me-nots (Boraginaceae), *Daucus*, *Eriastrum*, *Silene, Plantago,* and six-weeks fescue (*Vulpia octoflora*). Prominent non-native annuals included red brome.

At 975 masl near the ignition point, the fire died out where the north slope lessened below a 20% incline, and foothill palo verde, brittlebush (*Encelia farinosa*), and saguaro became prominent. An air drop of fire retardant nearby may have played a role as well (**Figure 3B**).

One kilometer west at similar elevation, the fire reached a ridge with a warmer southwest exposure and a 0.04 km^2 patch of buffelgrass mixed with typical Arizona Upland vegetation, including palo verde, brittlebush, saguaro, canyon ragweed (*Ambrosia ambrosioides*), limber bush (*Jatropha cardiophylla*), and desert lavender (*Hyptis emoryi*). Another non-native bunchgrass, fountain grass, was also common. A fire crew had expertly cut a fuel break along the ridgeline, keeping the fire out of most of the *Cenchrus* (fountain and buffelgrass) and saguaros. On the burned side of the fire break, heat from the burning *Cenchrus* scorched and/or killed the native palo verde, brittlebush and saguaro, of which the brittle bush and saguaro do not resprout, and the palo verde resprouts weakly. These three species, emblematic of Arizona Upland Sonoran Desert, were burned more severely by the *Cenchrus* as compared to those places where the fire was fueled by winter annuals, due to difference in fuel loading (see McDonald and McPherson, 2013).

On the south side of the Catalinas our surveys revealed a similar suite of winter annual plants fed by rains during the winter of 2019–2020 providing continuous fine fuels on the more mesic north aspects in desert areas. The fire followed these fuels and those in the Semi-desert Grassland downhill in the southwest corner of the fire (**Figure 3**). At the upper elevations of desert habitats and in desert grassland areas, extensive shindaggers (*Agave schottii*) and Lehmann's lovegrass provided continuous fuels bridging these ecosystems with the Oak Woodland and Chaparral.

Further downslope, and on the more xeric sides of ridges (south-facing slopes), winter annuals were less abundant among the palo verde, saguaro, brittlebush, and baby bonnets (*Coursetia glandulosa*) of the Arizona Upland. This ecosystem mostly escaped the flames on the south side of the Catalinas, except where the fire was carried by patches of buffelgrass and fountain grass at densities greater than 50% cover. Such patches were generally small and discontinuous along rocky hillsides, limiting the fire's extent into Desertscrub. Large patches of buffelgrass (as mapped in 2018) were close to the Bighorn Fire perimeter (**Figure 3**), but the flames were backing downslope and died before reaching these patches from a lack of continuous fuels and presumably unfavorable winds at night.

Buffelgrass Infestation

Within the front range of the Catalinas we mapped 6,485 patches of buffelgrass totaling 4.43 km^2, spanning an elevation range of 839 to 1,476 masl as of 2018. At the interface of desert and grassland the distribution of buffelgrass is best characterized as a mosaic of small, isolated patches. Moving downslope, these patches grow in size and coalesce into stands of buffelgrass that cover entire slopes (**Figure 4**). In addition, the density of buffelgrass within patches increases as elevation decreases. The distribution of buffelgrass in relation to aspect exhibits a similar pattern, with south- and southwest-facing aspects favoring the growth of larger, denser patches of buffelgrass than north- and northeast-facing aspects, which can often be entirely free of buffelgrass, at present. Most (94.6%) of the buffelgrass was found on south-facing slopes with slightly higher (50.6%) on southwest- than southeast-facing slopes (44.1%). The distribution of patch sizes was highly skewed, with just the largest seven patches comprising 25.5% of all digitized buffelgrass (**Supplementary Table 3**). The largest patch was 0.34 km^2 (7.8% of all buffelgrass) and a total of 129 discrete patches were at least one acre in size. The distribution of buffelgrass along the elevational profile indicates that the most heavily invaded area is upslope from the WUI and downslope from the ecotone between the Arizona Upland and the higher elevation desert grassland (**Figure 4**).

Species Responses to the Fire

Saguaros

We recorded 95 saguaros in the ten plots in the fire zone and 40 saguaros in the five control plots. About 94% of the saguaros in the fire zone had some fire injury; 41% had greater than 50% of the skin surface injured by the fire; and 29% had fire injury covering greater than 80% of their surface (**Figure 5**). The overall first-year mortality of saguaros sampled in the fire zone was 18% (17 of the 95 individuals), the majority of which are young plants. Fifteen of the seventeen dead saguaros had a height less than 2 meters. There was strong spatial variation in saguaro mortality within the fire zone. The plot mean mortality ranged from zero in four of the plots to 80% in one plot (**Supplementary Figure 5**). The percent of skin damaged by the fire had a significant negative relationship with the height of a saguaro ($\chi_1^2 = 35.65$, $p = 2.36\text{e-}09$; **Figure 5**).

Based on the results from Esque et al. (2004), who predicted saguaro mortality six years after the fire, our one-year post-fire results show a two-step nonlinear relationship with the range of fire injury occurring on plant surface (**Figure 6**). Conservatively, a 50 percent chance of death is associated with approximately 85% range of fire injury. Based on this prediction, 36% of the live saguaros surveyed in the Mercer Fire zone will have a 50 percent or greater chance of dying in the future. It should be noted that high humidity during the Mercer Fire raised dead fuel moisture and dampened fire behavior, compared to fire behavior surrounding the saguaros that we examined in the Bighorn Fire.

Vegetation Plots

At the initial post-burn time step, species richness was significantly lower in burned plots than in the control plots in both the Arizona Upland Sonoran Desertscrub (p = 0.0447) and the Semi-desert Grassland (p = 0.0063; **Figure 7**). Likewise, vegetation cover is much less in burned areas than unburned areas immediately after the fire (**Figure 8**), and the majority of the remaining cover in burned areas is from dead plants.

The cover of plants observed in control plots provides some indication of the fuels present that carried the Bighorn Fire in this area. The control plots in the Semi-desert Grassland had high (approximately 50%) cover of dead annual plants, mostly from the 2019–2020 winter-spring growing season. Predominant annuals were the natives *Aristida adscensionis*, *Cryptantha* sp., *Daucus pusillus*, *Lepidum* sp., *Plantago patagonica*, *Silene antirrhina*, *Stylocline micropoides*, and *Vulpia* sp., and the non-native red brome, with all the natives roughly equaling the red brome biomass. Remnant winter annuals were much less dense in the Arizona Upland Sonoran Desertscrub, with less than 5% total cover in that vegetation type.

Most perennial species observed in the plots exhibited at least some regrowth four months post-fire (**Figure 9**). Many of the most common perennial desert species, including fairy-duster (*Calliandra eriophylla*), limberbush, slender janusia (*Cottsia gracilis*), and littleleaf ratany (*Krameria erecta*), all had high rates of survival and regrowth with over 75% of living individuals showing post-fire regrowth. Ocotillo had an initial survival rate of over 90% in both vegetation types, but few individuals had visible post-fire regrowth. However, some larger shrubs and trees appear to have survived at lower rates. Foothill palo verde, which commonly grows as a short-statured tree in Arizona Uplands Sonoran Desertscrub, suffered 68% mortality in that vegetation type, and 80% in the Semi-desert Grassland where it is also present but far less common. Resprouting from the base was observed in this species. Similarly, velvet mesquite, which is more common in the Semi-desert Grassland, suffered approximately 50% top-kill across both vegetation types, again with some individuals resprouting from the base. Hopbush, a large shrub present in both vegetation types, suffered near total mortality with only one surviving individual in the burned Semi-desert Grassland plots. Cacti generally suffered extremely high mortality, with only a few individuals of Engelmann prickly pear (*Opuntia engelmannii*), Graham's fishhook cactus (*Mammillaria grahamii*), hedgehog cactus (*Echinocereus* spp.), and Christmas cholla (*Cylindropuntia leptocaulis*) surviving. Notably, no saguaros survived in the burned Arizona Upland Sonoran Desertscrub plots.

Perennial grasses appeared to suffer high initial mortality due to the fire in both vegetation types, but the observed absence of regrowth is likely due to the abnormal lack of summer 2020 monsoon rains, with potential for regrowth still possible. The Semi-desert Grassland had generally low coverage of perennial grasses (**Figure 8**), which included the natives purple three-awn, spider grass, sideoats grama, slender grama (*Bouteloua repens*), tanglehead (*Heteropogon contortus*), and bush muhly, and less frequently Lehmann's lovegrass and no buffelgrass. In the Arizona Uplands Sonoran Desertscrub, perennial grasses had a negligible contribution to vegetation cover, though a high number were observed in the burned plots (**Figure 9**). It is possible that invasive grasses were present in the burned Sonoran Desertscrub and not in the control area. Future monitoring of these long-term plots will address this uncertainty.

State-and-Transition Fire-Spread Models

The simulation began with 4.4 km^2 of buffelgrass produced by the mapping effort (see Sections "Mapping buffelgrass infestation" and "Buffelgrass infestation") and after 30 years resulted in an average of 49.2 km^2 invaded by buffelgrass (range 42.9–55.2 km^2; sd 3.34). Buffelgrass patches with $>$50% cover that burned in simulations resulted in an average of 23 km^2 (range 1.1–41.8 km^2; sd 11) of the landscape converted to a state where the majority of native vegetation is not expected to persist at the end of 30 years, although this was highly stochastic. With the presence of buffelgrass, the study area is likely to experience larger fires with greater area burned over the 30-year period (**Figure 10**). This impact is evident as more continuous buffelgrass is present on the landscape, with a noticeable increase in fires after 20 years, ca. 2040 (**Figure 10**). The simulations also showed a greater annual burned area below 1,200 masl in elevation in the scenario with buffelgrass (**Figure 10**).

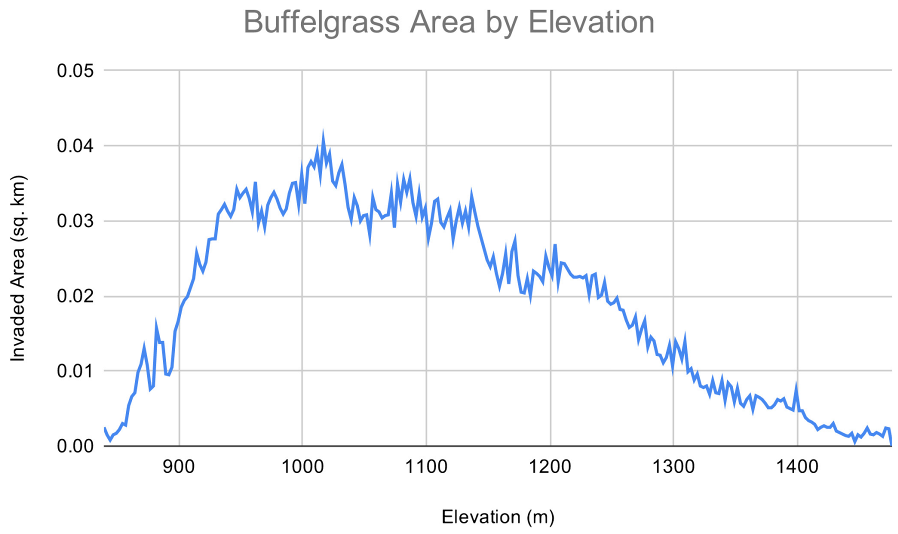

FIGURE 4 | Buffelgrass coverage by elevation. Note the elevation with most buffelgrass coverage is above the wildland-urban interface (900–950 masl), but below the Desertscrub/Semi-desert Grassland ecotone (1,200 masl).

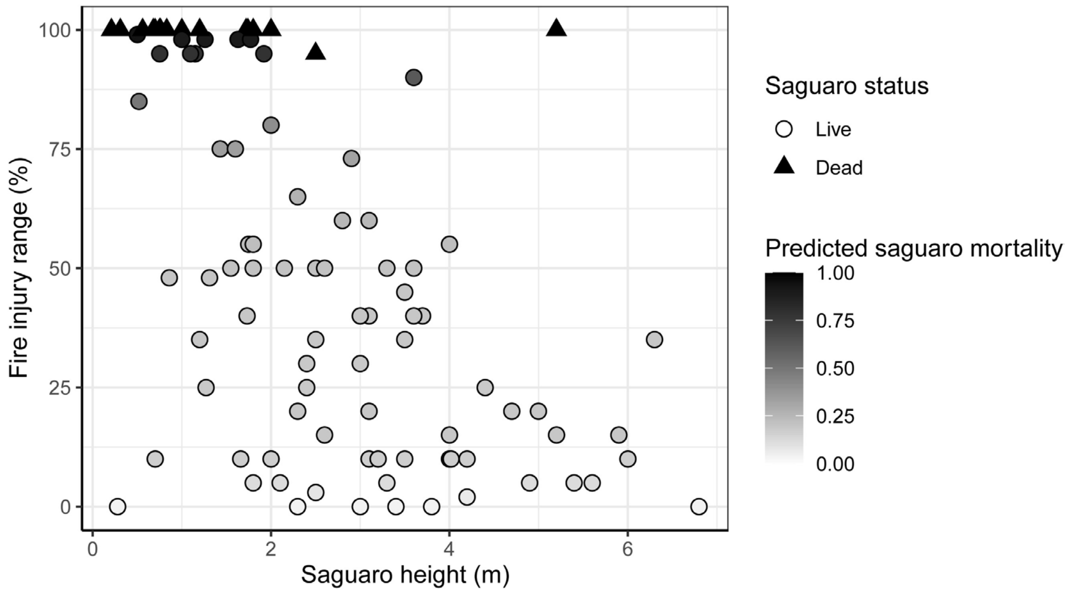

FIGURE 5 | Impacts of fire on saguaros (*Carnegiea gigantea*). The relationship between individual saguaro height and the range of injury by the Mercer Fire. Dead saguaros are shown in black triangles, live saguaros are shown in circles with the grayscale gradient indicating future mortality probability of each saguaro based on the range of fire injury.

Without mitigation, buffelgrass can be expected to continue to spread and increase in abundance. The presence and spread of buffelgrass in the Catalina Mountains will result in larger fires, more area burned resulting in the loss of native species (as a result of the converted area) and more fires burning into the desert ecosystem and toward residential housing at the WUI.

Resident Perceptions

Of the 550 survey respondents, 36 were evacuated during the Bighorn Fire, 109 had friends or family members who were evacuated, and 47 reported loss of recreation access due to the fire. In the full sample, 53% of respondents reported that they had heard of buffelgrass. Awareness of buffelgrass was significantly higher among those evacuated ($p = 0.0080$) and those who lost recreation access ($p = 0.0023$), but was not significantly different among those whose family or friends were evacuated ($p = 0.5728$).

When asked to rank their awareness of buffelgrass-related threats on a scale from 1 to 10, respondents reported average awareness of 4.63 for fire risk, 3.05 for saguaro loss, and 2.78

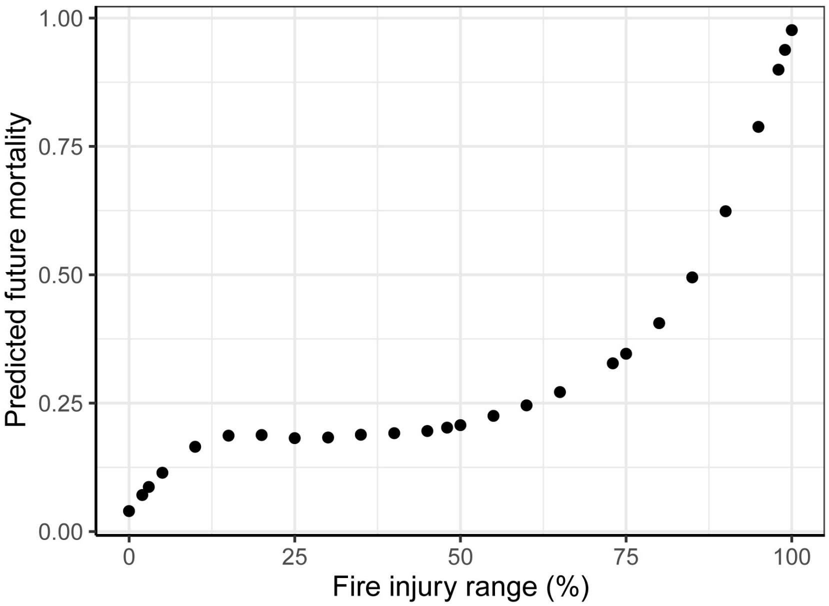

FIGURE 6 | Predicted mortality of saguaros (*Carnegiea gigantea*) post-fire. The range of fire injury of saguaros surveyed in the Mercer Fire site gives the prediction of their future mortality. The prediction is based on a relationship presented Esque et al. (2004).

for declining property values. Evacuated respondents reported significantly higher awareness of fire risk (p = 0.0228), saguaro loss (p = 0.0001), and declining property values (p = 0.0001). Those who lost recreation access reported significantly higher awareness of fire risk (p = 0.0028) and saguaro loss (p = 0.0279) but reported no greater awareness of property loss (p = 0.1089). Awareness of threats was not significantly different among those whose family or friends were evacuated.

DISCUSSION

The Bighorn Fire occurred at what is perhaps an inflection point in time. The fire started at an elevation just above the desert, ca. 1,200 masl, and it generally did not drop below this elevation into the desert lowlands, especially on more arid south-facing slopes (**Figure 3B**). The role of invasive grasses in carrying the fire, including buffelgrass, fountain grass, and Lehmann's lovegrass was limited by their patchy distribution at the Desertscrub/Semi-desert Grassland ecotone at 1,200 masl. The Bighorn Fire moved downslope at night, with limited energy release. This allowed bare ground in desertscrub, hiking or game trails, and rock outcrops, to serve as fuel breaks, preventing further spread downslope. As shown by our state-and-transition models, rapid and continued spread and coalescence of buffelgrass patches will increasingly create a buildup of fuels and link the Desertscrub and Semi-desert Grassland communities (**Figure 10**). Even with the current densities, a lightning strike or human ignition further downslope, as with the 2020 Bush Fire in Central Arizona, could have ignited a fire in Sonoran Desertscrub much larger than the 2019 Mercer Fire. In many respects, the Bighorn Fire was a near miss for the Catalina Foothills WUI.

Slope exposure strongly influenced the behavior of the Bighorn Fire at lower elevations. While the south-facing slopes were largely untouched, substantial areas of north-facing slopes and north-trending piedmonts below 1,200 masl were burned due to a higher fuel load of dried winter annuals (**Figure 3B**, top half of figure). On these north-facing slopes, the Bighorn Fire did spread within saguaro-palo verde habitat. The Desertscrub/Semi-desert Grassland ecotone receives more winter rainfall and has experienced an increase in grass coverage (native and non-native; Turner et al., 2003) with reduced grazing pressure. These conditions are somewhat analogous to other productive desert shrubland areas that sustained large fires in 2005 and 2020 such as central Arizona (Cave Creek and Bush Fires) and the eastern California (2005 Hackberry and 2020 Dome Fires). El Niño rain events provide pulses of moisture and nutrients that lead to a profusion of annual plant growth, both native and non-native, that dry out in arid foresummer and meet the minimum fuel loads (~100 g/m^2) required to drive "grassland fire" (Scott and Burgan, 2005). Increase in the freeze-free season, increased frequency of wet winters, and an earlier onset and lengthening of the fire season are predicted to further the fire-invasive feedback loop in the western United States (Abatzoglou and Kolden, 2011).

In the Bighorn Fire, fire spread across the Desertscrub/Semi-desert Grassland ecotone was influenced by densities of both winter and perennial annual grasses interacting with landscape structure, including elevation and slope exposure, degree, roughness, and the occurrence of animal and human trails, which acted as minor fuel breaks. In some ways, this parallels the way that forest fires percolate with landscape structure higher up in the Santa Catalina Mountains (Iniguez et al., 2008). In Arizona Upland habitat, mechanical and chemical treatment options to control invasive grasses, and other management decisions (e.g.,

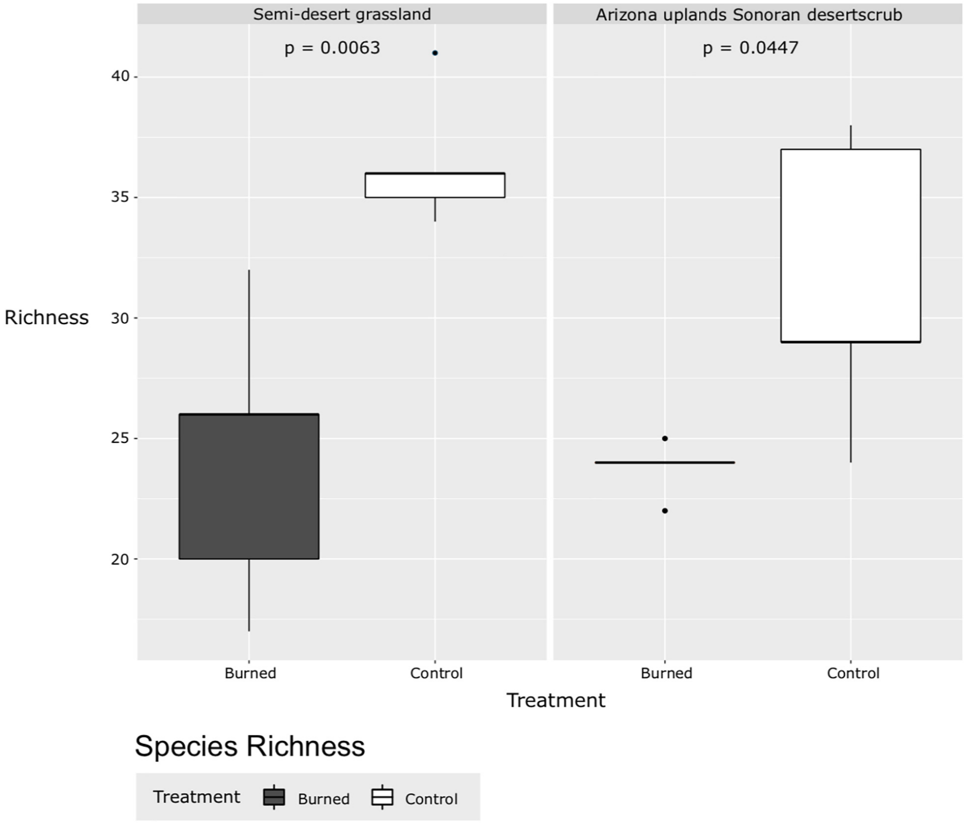

FIGURE 7 | Species richness of burned and control plots, Catalina State Park, Tucson, Arizona.

placement of new hiking trails) to prevent cross-biome fire spread could be prioritized according to landscape structure, phenology of the invasive grass (and uptake of herbicides), and predicted fire behavior (Bean, 2014; Thistle et al., 2014). This prioritization could also apply to the air drop of flame retardant by fixed wing aircraft during wildfires, as well as to the pinpoint application of herbicides from rotary wing aircraft, in the steep and inaccessible terrain of the Catalina piedmont (Bean, 2014; Thistle et al., 2014).

Despite evidence from other post-fire studies in the Sonoran Desert (Cave, 1982; McLaughlin and Bowers, 1982; Cave and Patten, 1984; Rogers, 1986; Loftin, 1987; Wilson et al., 1995; Alford et al., 2005; Shryock et al., 2015), we were surprised by the high number of desert species with resprouting capacity (**Figure 9**). This result begs the question of the adaptive origin of this behavior and if there is a fire history within the desert as suggested by some authors (e.g., Brown and Minnich, 1986). Much of the flora of the semi-tropical Sonoran Desert is evolved from thornscrub or dry forest environments (Axelrod, 1979). In the tropics and tropical dry forests, resprouting is a common and persistent strategy (Poorter et al., 2010), where fire is rare to absent, and is often in response to stressors such as hurricanes (Paz et al., 2018) and freezes (Bojoìrquez et al., 2019). It has also been indicated, but less clearly, that resprouting is common in areas with low site productivity such as arid environments as a possible response to drought (Vesk and Westoby, 2004). It seems that, rather than being an adaptation to fire itself in these desert species, resprouting is a response to variable causes of stress damage. The degree of resilience offered by resprouting capacity is unclear and likely not robust after repeated burns. In burned areas in the Mojave Desert, community composition remains stable in creosote (*Larrea tridentata*) dominated communities post-fire (Engle and Abella, 2011), though there is a marked decrease in structure and keystone species (Abella et al., 2009; Engle and Abella, 2011). It will be critical to monitor and track the long-term recovery and trajectory of community composition in multiple burned sites throughout the desert lowlands impacted by fire.

Conceptual state-and-transition models have been used to evaluate ecosystem changes applicable to a broad swath of landscape types (e.g., Cobb et al., 2017), and fire simulations have predicted vegetation changes (e.g., Conlisk et al., 2015). There are also many examples of invasive species spread models to determine their potential impact on fire risk, but without simulating fire (Wang et al., 2016). There are few examples, however, that combine simulations of the spread of invasives and associated wildfires. The types of simulations we used couple a state-and-transition model that simulates both the spread and increase in abundance of an invasive plant with a fire behavior model that allows exploration of the consequences of a non-native species that introduces

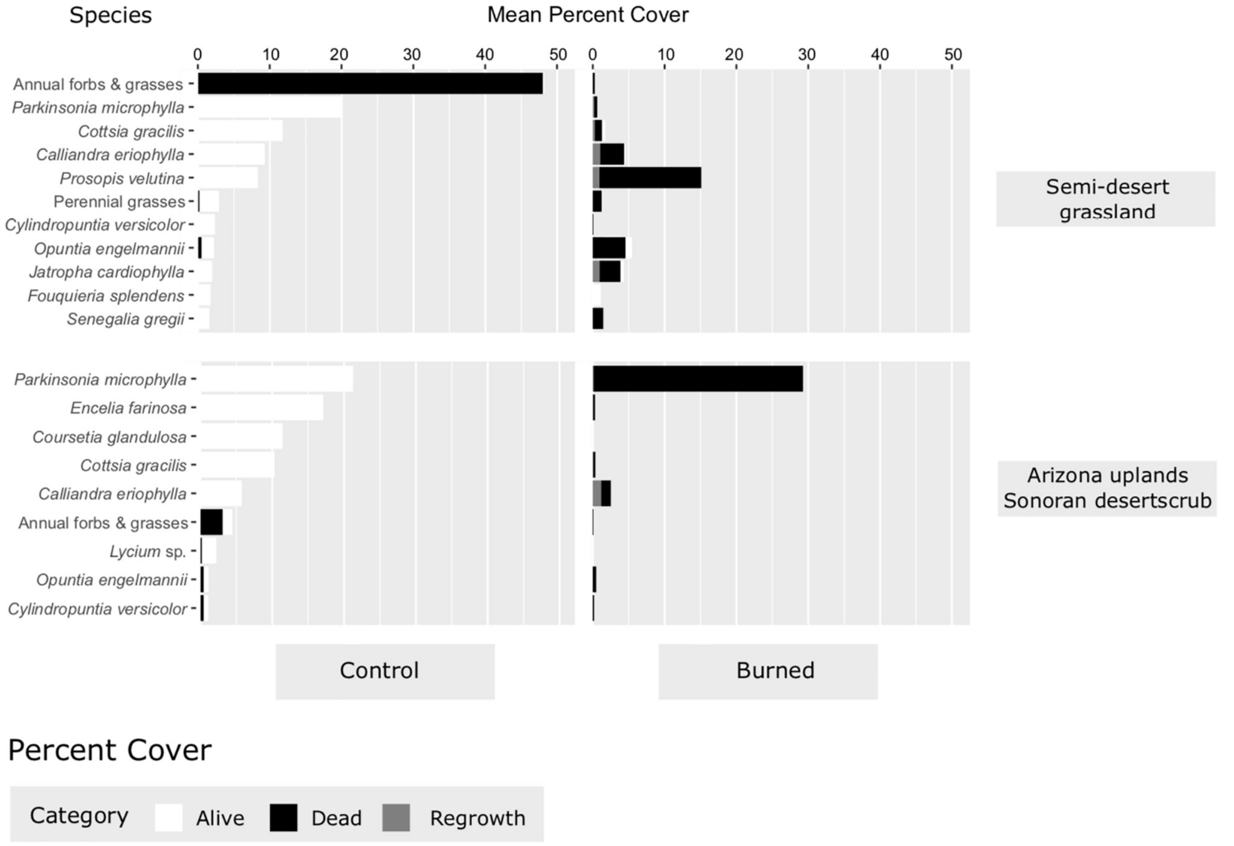

FIGURE 8 | Percent cover of the most prominent species in burned and control plots, Catalina State Park, Tucson, Arizona.

non-analog conditions (**Supplementary Figure 3**; Jarnevich et al., 2019). These combined models allow for the co-production of simulations by scientists, land managers, policy makers and the interested public; the consideration of additional drivers (e.g., climate variability and change); and the incorporation of alternative management actions and their timing across multiple jurisdictions (e.g., Miller et al., 2017). For land managers who are facing unprecedented changes in wildland fuel complexes at an exponential rate, these products provide some basis for weighing options. Actions delayed in such a situation greatly increase future costs and decrease the odds of achieving management goals, increasing the likelihood of a cascading series of undesirable events.

Southern and central Arizona, where buffelgrass is spreading rapidly, encompass two large metropolitan areas (Tucson and Phoenix), two major universities, a vibrant multi-billion-dollar tourism industry reliant on a unique ecological backdrop, and expansive public lands – from world-renowned national parks and monuments to military facilities vital to national defense. During the past two decades, a cross-jurisdictional effort was mounted to identify, communicate, and address the ecological and socioeconomic risks posed by buffelgrass invasion, with mixed success (Brenner and Franklin, 2017; Lien et al., 2021). Despite this sustained and coordinated public messaging campaign, local and regional actions continue to fall short of controlling the expanding front of invasive grass species in the region.

The survey results presented here are in general agreement with a 2017 survey of Homeowner Association (HOA) members in Tucson (Plecki et al., 2021). Most 2017 survey respondents were aware of buffelgrass, but their knowledge of mitigation strategies were limited. Likewise, our results suggest that while a majority of residents know about buffelgrass, many have limited awareness of its impacts on fire, desert plants, and property values. Awareness of these impacts is significantly higher among those who were personally affected by the Bighorn Fire. This suggests that over time, shifting fire regimes will increase residents' awareness of buffelgrass and demand for buffelgrass mitigation. However, the ability to respond to and manage the altered ecological state of recurring fires will likely be insufficient to mitigate the economic and biodiversity fallout without prompt action.

CONCLUSION

Timely case studies of extreme ecological events like the Bighorn Fire are essential, not only to understand causes and project consequences in the short and the long term, but also to inform management and policy responses and galvanize public attention.

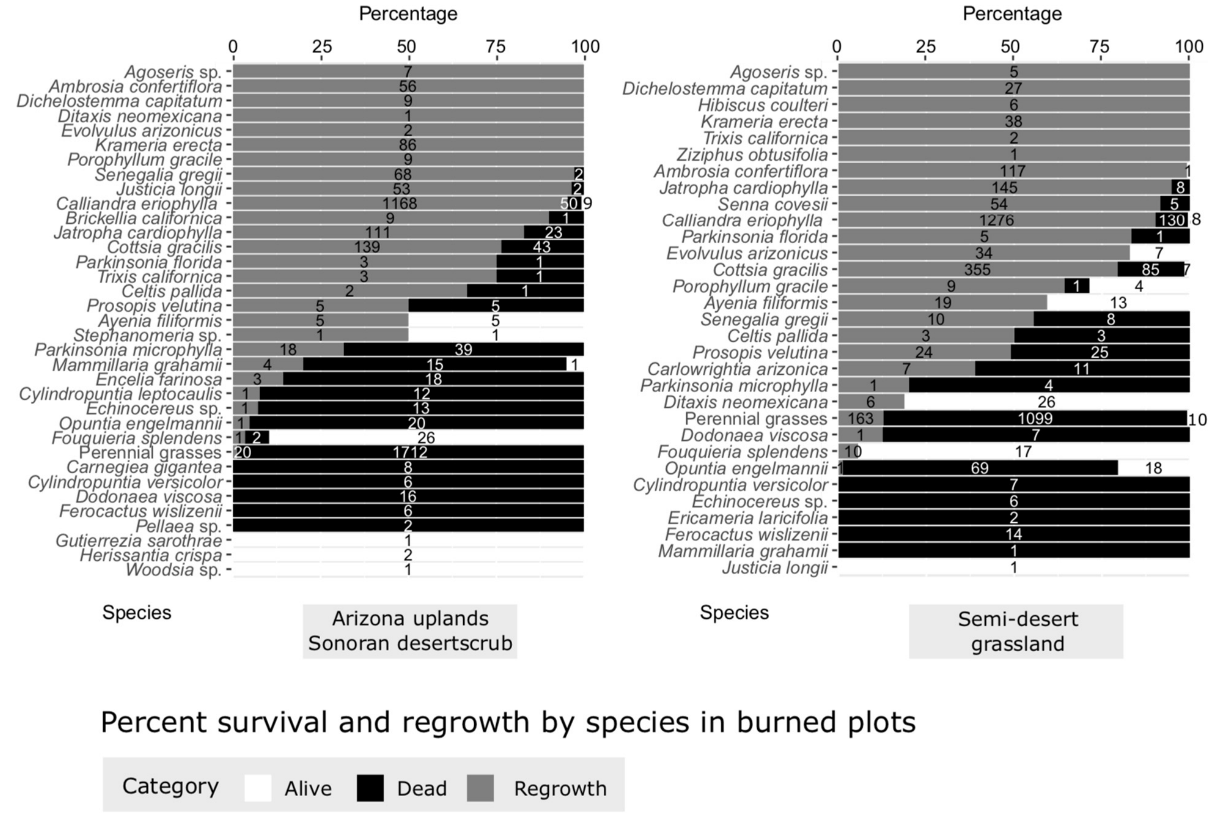

FIGURE 9 | Percent survival and regrowth of species in burned plots, Catalina State Park, Tucson, Arizona.

We are already witnessing a dramatic shift in the fire regimes of North American deserts, the scope of which is amplifying and increasingly impacting ecosystem processes and the WUI at the landscape-level. Real time assessment of these fire events and their aftermaths using empirical, modeling, and multidisciplinary approaches can lead to a refined understanding of the driving mechanisms of shifting states. Public attention and political willingness to act are likely to decay quickly after extreme events like the Bighorn Fire, and time is of the essence for the effective transfer of any actionable knowledge. As the pace of change accelerates, the continuous establishment of baselines and benchmarks will allow an iterative unpacking of novel states and conditions.

For example, increasing connectivity between desert valleys and the uplands is altering the relationship between hydroclimatic variability and annual area burned. In the southwestern United States, El Niño events are normally associated with more winter-spring precipitation and reduced fire occurrence in the uplands (Swetnam and Betancourt, 1990). By contrast, in central Arizona more frequent and severe fires in Sonoran Desert vegetation occur after abnormally wet winter/spring precipitation associated with both strong and weak El Niño events (1978–1979, 1987–1988, 1991–1995, 2004–2005, 2018–2019, and 2019–2020) and also during the positive phase of the Pacific Decadal Oscillation (1976–1995). In Tonto National Forest, annual area burned in Sonoran Desert vegetation was influenced by greater than normal precipitation in two and three consecutive winters (Rogers and Vint, 1987; Alford et al., 2005), which tend to happen during multi-year El Niño events. The copious winter rainfall initiated broadly synchronous blooms of red brome and other invasive winter annual grasses across the Sonoran (and Mojave) Desert, which then dried out and burned in the ensuing summer. The wide ignition fronts from wildfires driven by winter annual plants tend to travel upslope with convection and spread into forests at a time when the forests normally would not burn. By contrast, buffelgrass and other summer-flowering perennials can fuel wildfires and desert-forest connectivity in any given year, regardless of winter precipitation variability. The relationship between interannual and decadal climate variability and fire activity across all biomes could shift significantly in the near future.

A coalescing front of invasive perennial and annual grasses are creating increased connectivity between the desert and forests on mountain slopes that will likely drive heightened fire risk at the WUI in the coming decades. Future efforts aimed at better understanding the history of fire in the desert, the resiliency of desert species to fire, the association between fire and ENSO and other climatic events, social studies that address the perception of change, sustained mapping efforts, an assessment of the effectiveness of fuel breaks in limiting connectivity, and

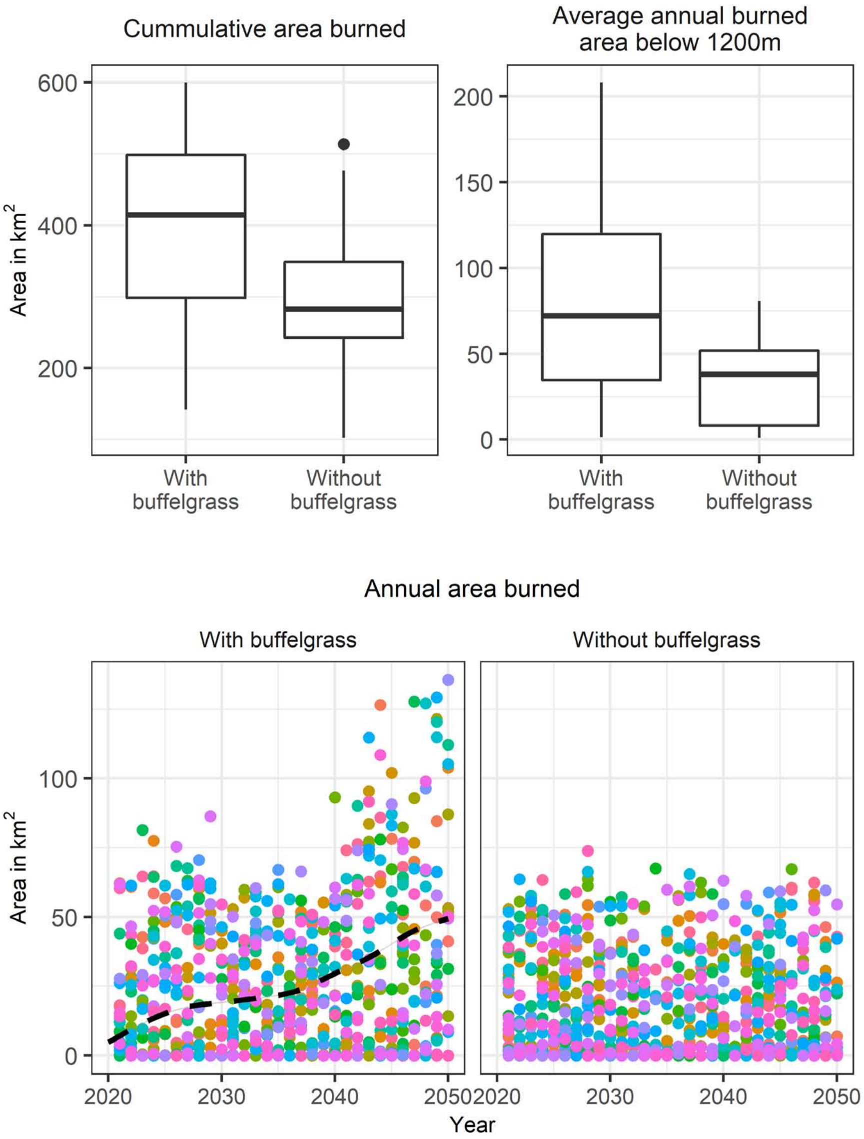

FIGURE 10 | State-and-transition fire-spread models. Box plots and time series of 50 Monte Carlo simulations across a 30-year time horizon simulating fire for two scenarios, with and without buffelgrass spreading across the landscape. Box plots include average annual burned area below 1,200 masl and cumulative burned area over the 30-year period. Time series (bottom panels) are annual area burned colored by different Monte Carlo simulations for each simulation year for the two scenarios with the black line representing the average annual area invaded by buffelgrass over the course of the simulation.

focused invasive species control will all provide an enhanced knowledge base and management actions to address this fast-evolving fire risk.

DEDICATION

We dedicate this paper in memory of our friend and colleague Travis M. Bean who passed away unexpectedly on May 27, 2020. Travis was instrumental in launching efforts to address and manage large scale ecosystem changes driven by invasive perennial grasses in desert environments. His commitment and joyful nature will be sorely missed.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BTW, CSJ, KAF, PG, KAH, JM, and JLB initiated the manuscript and conceptualized its components. AO undertook and led the buffelgrass mapping effort. BTW, JSB, KAF, PG, JM, YML, JAR, and MRS undertook field work and data analyses. EB, ASMGK, AML, AP, and JRS completed the survey. BTW and JLB led writing efforts, with contributions from all authors. All authors reviewed and edited a complete draft of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.655561/full#supplementary-material

Supplementary Figure 1 | Areas visited in the Santa Catalina Mountains at the perimeter of the Bighorn Fire in the fall of 2020.

Supplementary Figure 2 | Comparison of digitization efforts based on Google Earth imagery (2018) and helicopter survey (2016) in the Santa Catalina Mountains, east of Sabino Canyon Recreation Area. Previous aerial survey boundaries shown in black have large, circular boundaries, both overestimating patch sizes and underestimating buffelgrass distribution. **(A)** Map showing numerous helicopter-surveyed patches in comparison to the Google Earth survey. **(B)** Map showing a single helicopter patch in comparison to the more numerous and complex boundaries of hand-digitized polygons from Google Earth. **(C)** A single patch identified from Google Earth imagery that was not mapped in the 2016 survey.

Supplementary Figure 3 | State-and-transition fire-spread model diagram. **(A)** State classes defined for the simulation, where uninvaded and seedbank are replicated for each fuel model class. **(B)** How growth transitions occur deterministically based on amount of time in the state class interacting with a "wet year" (probability of 26.7%) increase in age to decrease the overall amount of time required to transition to the next cover level.

Supplementary Figure 4 | State-and-transition fire-spread model study area including the fuel models used in the simulation and the 1,200 masl contour used to explore changes in low elevation fires caused by buffelgrass presence.

Supplementary Figure 5 | Locations of sampling plots established to assess saguaro mortality after the 2019 Mercer Fire. Ten plots were established within the zone of fire impact outlined in red. Five control plots were established outside of the fire zone. Circle size indicates the abundance of saguaros within each 20 × 20 m square plot. Grayscale indicates the degree of saguaro mortality in each plot.

Supplementary Table 1 | LANDFIRE mapped fuel loadings used in the simulation.

Supplementary Table 2 | FARSITE parameter values used in all simulations within SyncroSim.

Supplementary Table 3 | Patch sizes of the 10 largest buffelgrass patches compared to all other patches combined on the south slope of the Santa Catalina Mountains.

REFERENCES

Abatzoglou, J. T., and Kolden, C. A. (2011). Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. *Rangel. Ecol. Manag.* 64, 471–478. doi: 10.2111/rem-d-09-00151.1

Abatzoglou, J. T., and Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci. U.S.A.* 113, 11770–11775. doi: 10.1073/pnas.1607171113

Abella, S. R., Engel, E. C., Lund, C. L., and Spencer, J. E. (2009). Early post-fire plant establishment on a Mojave Desert burn. *Madroño* 57, 137–148. doi: 10.3120/0024-9637-56.3.137

Alford, E. J., Brock, J. H., and Gottfried, G. J. (2005). "Effects of fire on Sonoran Desert plant communities," in *Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II Proc. RMRS-P-36*, eds G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster (Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station), 451–454.

Axelrod, D. I. (1979). Age and origin of the Sonoran Desert. *Cal. Acad. Sci. Occas. Pap.* 13, 1–74.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.

Bean, T. M. (2014). *Tools for Improved Management of Buffelgrass in the Sonoran Desert.* Ph.D. Dissertation Thesis. Tucson, ARI: University of Arizona.

Betancourt, J. L. (2012). "Reflections on the relevance of history in a nonstationary world," in *Historical Environmental Variation in Conservation and Natural Resource Management*, eds J. A. Wiens, G. D. Hayward, H. D. Safford, and C. Giffen (New York, NY: Wiley-Blackwell), 307–318. doi: 10.1002/9781118329726.ch23

Betancourt, J. L. (2015). Energy flow and the 'grassification' of desert shrublands. *Proc. Natl. Acad. Sci. U.S.A.* 112, 9504–9505. doi: 10.1073/pnas.1512078112

Bojoìrquez, A., Aìlvarez-Yeìpiz, J. C., Buìrquez, A., and Martiìnez-Yriìzar, A. (2019). Understanding and predicting frost-induced tropical tree mortality patterns. *Global Change Biol.* 25, 3817–3828. doi: 10.1111/gcb.14775

Brenner, J. C., and Franklin, K. A. (2017). Living on the edge: emerging environmental hazards on the peri-urban fringe. *Environment* 59, 16–29. doi: 10.1080/00139157.2017.1374793

Brooks, M. L. (1999). Alien annual grasses and fire in the Mojave Desert. *Madroño.* 46, 13–19.

Brooks, M. L., and Pyke, D. A. (2001). "Invasive plants and fire in the deserts of North America," in *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management*, eds K. E. M. Galley and T. P. Wilson (Tallahassee, FL: Tall Timbers Research Station), 1–14.

Brooks, M. L., and Chambers, J. C. (2011). Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangel. Ecol. Manag.* 64, 431–438. doi: 10.2111/rem-d-09-00165.1

Brooks, M. L., Chambers, J. C., and McKinley, R. A. (2013). "Fire history, effects, and management in southern Nevada," in *The Southern Nevada Agency Partnership Science and Research Synthesis: Science to support land management in Southern Nevada - Executive Summary Gen. Tech. Rep. RMRS-GTR-304*, eds J. C. Chambers, M. L. Brooks, B. K. Pendleton, and C. B. Raish (Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station), 25–34.

Brown, D. E., and Minnich, R. A. (1986). Fire and changes in creosote bush scrub of the western Sonoran Desert. *Cal. Am. Midland Natural.* 116, 411–422. doi: 10.2307/2425750

Brusca, R. C., and Moore, W. (2013). *A Natural History of the Santa Catalina Mountains, Arizona with an Introduction to the Madrean Sky Islands.* Tucson, ARI: Arizona-Sonora Desert Museum Press.

Cave, G. H. (1982). *Ecological Effects of Fire in the Upper SONORAN Desert.* Thesis. Tempe, AZ: Arizona State University.

Cave, G. H., and Patten, D. T. (1984). Short-term vegetation responses to fire in the Upper Sonoran Desert. *J. Range Manag.* 37, 491–496. doi: 10.2307/3898842

Clark, C. (2006). *The Year We Lost the Desert. Earth Island Journal*. Available online at: https://www.earthisland.org/journal/index.php/magazine/entry/the_year_we_lost_the_deserts/ (accessed January 18, 2021).

Cobb, R. C. K., Ruthrof, X., Breshears, D. D., Lloret, A. F. T., Adams, H. D., Anderegg, W. R. L., et al. (2017). Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. *Ecosphere* 8:e02034. doi: 10.1002/ecs2.2034

Conlisk, E., Syphard, A. D., Franklin, J., and Regan, H. M. (2015). Predicting the impact of fire on a vulnerable multi-species community using a dynamic vegetation model. *Ecol. Modell.* 301, 27–39. doi: 10.1016/j.ecolmodel.2015.02.004

D'Antonio, C. M., and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87. doi: 10.1146/annurev.es.23.110192.000431

Daniel, C., Frid, L., Sleeter, B., and Fortin, M.-J. (2016). State-and-transition simulation models: a framework for forecasting landscape change. *Methods Ecol. Evol.* 7, 1413–1423. doi: 10.1111/2041-210x.12597

Elkind, K., Sankey, T. T., Munson, S. M., and Aslan, C. E. (2019). Invasive buffelgrass detection using high-resolution satellite and UAV imagery on Google Earth Engine. *Remote Sens. Ecol. Conserv.* 5, 318–331. doi: 10.1002/rse2.116

Engle, E. C., and Abella, S. R. (2011). Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *J. Appl. Ecol.* 48, 1401–1410. doi: 10.1111/j.1365-2664.2011.02057.x

Esque, T. C., Schwalbe, C. R., Haines, D. F., and Halvorson, W. L. (2004). Saguaros under siege: invasive species and fire. *Desert Plants* 20, 49–55.

Esque, T. C., Schwalbe, C., Lissow, J. A., Haines, D. F., Foster, D., and Garnett, M. C. (2007). Buffelgrass fuel loads in Saguaro National Park, Arizona, increase fire danger and threaten native species. *Park Sci.* 24, 33–56.

Finney, M. A. (2004). *FARSITE: Fire Area Simulator–Model Development and Evaluation Research Paper RMRS-RP-4*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Franklin, K. A., Lyons, K., Nagler, P. L., Lampkin, D., Glenn, E. P., Molina-Freaner, F., et al. (2006). Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. *Biol. Conserv.* 127, 62–71. doi: 10.1016/j.biocon.2005.07.018

Frid, L., and Wilmshurst, J. F. (2009). Decision analysis to evaluate control strategies for crested wheatgrass (*Agropyron cristatum*) in Grasslands National Park of Canada. *Invasive Plant Sci. Manag.* 2, 324–336. doi: 10.1614/ipsm-09-006.1

Frid, L., Holcombe, T., Morisette, J. T., Olsson, A. D., Brigham, L., Bean, T. M., et al. (2013). Using state-and-transition modeling to account for imperfect knowledge in invasive species management. *Invasive Plant Sci. Manag.* 6, 36–47. doi: 10.1614/ipsm-d-11-00065.1

Fusco, E., Finn, J., Balch, J., Nagy, R. C., and Bradley, B. (2019). Invasive grasses increase fire occurrence and frequency across U.S. ecoregions. *Proc. Natl. Acad. Sci. U.S.A.* 116, 23594–23599. doi: 10.1073/pnas.1908253116

Grechi, I., Chadès, I., Buckley, Y. M. B., Friedel, M. H., Grice, A. C., Possingham, H. P., et al. (2014). A decision framework for management of conflicting production and biodiversity goals for a commercially valuable invasive species. *Agric. Syst.* 125, 1–11. doi: 10.1016/j.agsy.2013.11.005

Holmgren, C. A., Norris, J., and Betancourt, J. L. (2007). Inferences about winter temperatures and summer rains from the late Quaternary record of C4 perennial grasses and C3 desert shrubs in the northern Chihuahuan Desert. *J. Q. Sci.* 22, 141–161. doi: 10.1002/jqs.1023

Iniguez, J. M., Swetnam, T. W., and Yool, S. R. (2008). Topography affected landscape fire history patterns in southern Arizona, USA. *For. Ecol. Manag.* 256, 295–303. doi: 10.1016/j.foreco.2008.04.023

Iniguez, J. M., Swetnam, T. W., and Baisan, C. H. (2016). Fire history and moisture influences on historical forest age structure in the sky islands of southern Arizona, USA. *J. Biogeogr.* 43, 85–95. doi: 10.1111/jbi.12626

Jarnevich, C. S., Holcombe, T. R., Thomas, C. C., Frid, L., and Olsson, A. (2015). Simulating long-term effectiveness and efficiency of management scenarios for an invasive grass. *AIMS Environ. Sci.* 2, 427–447. doi: 10.3934/environsci.2015.2.427

Jarnevich, C. S., Thomas, C., Young, N. E., Backer, D., Cline, S., Frid, L., et al. (2019). Developing an expert elicited simulation model to evaluate invasive species and fire management alternatives. *Ecosphere* 10:e02730.

Jarnevich, C. S., Young, N. E., Thomas, C. D., Grissom, P., Backer, D., and Frid, L. (2020). Assessing ecological uncertainty and simulation model sensitivity to evaluate an invasive plant species' potential impacts to the landscape. *Sci. Rep.* 10:19069.

Koehler, P. A., Anderson, R. S., and Spaulding, W. G. (2005). Paleoenvironments of the mojave and colorado deserts during the late quaternary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 215, 297–311.

Landfire. (2020). *LANDFIRE Remap 2016 Scott and Burgan Fire Behavior Fuel Model (FBFM40) CONUS. LF Remap. Earth Resources Observation and Science Center (EROS)*. Sioux Falls, SD: U.S. Geological Survey.

Lien, A. M., Baldwin, E., and Franklin, K. A. (2021). Collective action and invasive species Governance in Southern Arizona. *Rangel. Ecol. Manag.* 74, 151–164. doi: 10.1016/j.rama.2020.10.004

Loftin, S. R. (1987). *Postfire dynamics of a Sonoran Desert ecosystem. Thesis*. Tempe, AZ: Arizona State University.

McAuliffe, J. R., and Van Devender, T. R. (1998). A 22,000-year record of vegetation change in the north-central Sonoran Desert. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 141, 253–275. doi: 10.1016/s0031-0182(98)00054-6

McDonald, C. J., and McPherson, G. R. (2013). Creating hotter fires in the Sonoran Desert: buffelgrass produces copious fuels and high fire temperatures. *Fire Ecol.* 9, 26–39. doi: 10.4996/fireecology.0902026

McLaughlin, S. P., and Bowers, J. E. (1982). Effects of wildfire on a Sonoran Desert plant community. *Ecology* 63, 246–248. doi: 10.2307/1937048

Merriam, C. H. (1890). Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado in Arizona. *North Am. Fauna* 3, 1–136. doi: 10.3996/nafa.3.0001

Miller, B. W., Symstad, A. J., Frid, L., Fisichelli, N. A., and Schuurman, G. W. (2017). Co-producing simulation models to inform resource management: a case study from southwest South Dakota. *Ecosphere* 8:e02020. doi: 10.1002/ecs2.2020

Noonan-Wright, E., Opperman, T. S., Finney, M. A., Zimmerman, T. G., Seli, R. C., Elenz, L. M., et al. (2011). Developing the U.S. Wildland Fire Decision Support System. *J. Combust.* 2011:14. doi: 10.1155/2011/168473

Olsson, A. D., Hannah, C., Hartfield, K., Orr, B. J., and Marsh, S. E. (2009). *Using Remote Sensing to Map and Manage Buffelgrass Infestations in the Tucson and Santa Catalina mountains. Final Report for the National Park Service. Arizona Remote Sensing Center Office of Arid Lands Studies, The University of Arizona*. Tucson, AZ: The University of Arizona.

Olsson, A. D., van Leeuwen, W. J., and Marsh, S. E. (2011). Feasibility of invasive grass detection in a desertscrub community using hyperspectral field measurements and Landsat TM imagery. *Remote Sens.* 3, 2283–2304. doi: 10.3390/rs3102283

Olsson, A. D., Betancourt, J. L., Crimmins, M. A., and Marsh, S. E. (2012a). Constancy of local spread rates for buffelgrass (*Pennisetum ciliare* L.) in the Arizona Upland of the Sonoran Desert. *J. Arid Environ.* 87, 136–143. doi: 10.1016/j.jaridenv.2012.06.005

Olsson, A. D., Betancourt, J. L., McClaran, M. P., and Marsh, S. E. (2012b). Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. *Divers. Distrib.* 18, 10–21. doi: 10.1111/j.1472-4642.2011.00825.x

Olsson, A. D., and Morisette, J. T. (2014). Comparison of simulated HyspIRI with two multispectral sensors for invasive species mapping. *Photogr. Eng. Remote Sens.* 3, 217–227. doi: 10.14358/pers.80.3.217

Parker, K. C. (2002). "Fire in the Pre-European Lowlands of the American Southwest," in *Fire, Native Peoples, and the Natural Landscape*, ed. T. R. Vale (Washington, DC: Island Press), 101–142.

Paz, H., Vega-Ramos, F., and Arreola-Villa, F. (2018). Understanding hurricane resistance and resilience in tropical dry forest trees: a functional traits approach. *Forest Ecology and Management* 426, 115–122. doi: 10.1016/j.foreco.2018.03.052

Pierson, E. A., Turner, R. M., and Betancourt, J. L. (2013). Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert. *J. Arid Environ.* 88, 57–69. doi: 10.1016/j.jaridenv.2012.08.008

Plecki, A. F., Akamani, K., Groninger, J. W., Brenner, J. C., and Gage, K. L. (2021). Homeowner perceptions and responses to buffelgrass invasion risk in the Tucson, Arizona Wildland-Urban Interface. *Heliyon* 7:e07040. doi: 10.1016/j.heliyon.2021.e07040

Poorter, L., Kitajima, K., Mercado, P., Chubiña, J., Melgar, I., and Prins, H. H. T. (2010). Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology* 91, 2613–2627. doi: 10.1890/09-0862.1

Rogers, G. F. (1986). Comparison of fire occurrence in desert and nondesert vegetation in Tonto National Forest. *Ariz. Madroño* 33, 278–283.

Rogers, G. F., and Vint, M. K. (1987). Winter precipitation and fire in the Sonoran Desert. *J. Arid Environ.* 13, 47–52.

Salo, L. F. (2005). Red brome (*Bromus rubens* subsp. madritensis) in North America: possible modes for early introductions, subsequent spread. *Biol. Invasions* 7, 165–180. doi: 10.1007/s10530-004-8979-4

Scott, J. H., and Burgan, R. E. (2005). *Standard Fire Behavior Fuel Models: A Comprehensive Set for use With Rothermel's Surface Fire Spread Model. Gen. Tech. Rep. RMRS-GTR-153*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Shryock, D. F., Esque, T. C., and Chen, F. C. (2015). *A 30-Year Chronosequence of Burned Areas in Arizona—Effects of Wildfires on Vegetation in Sonoran Desert Tortoise (Gopherus morafkai*) Habitats. U.S. Geological Survey Open-File Report, 2015-1060. Reston, VA: U.S. Geological Survey, doi: 10.3133/ofr20151060

Schmid, M., and Rogers, G. F. (1988). Trends in fire occurrence in the Arizona upland subdivision of the Sonoran Desert, 1955 to 1983. *Southwestern Nat.* 33, 437–444. doi: 10.2307/3672211

Swetnam, T. R., and Betancourt, J. L. (1990). Fire-Southern Oscillation relations in the southwestern United States. *Science* 24, 1017–1020. doi: 10.1126/science.249.4972.1017

Thistle, H. W., White, J. A., Backer, D. M., Ghent, J. H., Throop, W. E., Bean, T. M., et al. (2014). A buffelgrass aerial spraying pilot project: spray application and deposition. *Appl. Eng. Agric.* 30, 17–24. doi: 10.13031/aea.30.10232

Turner, R. M., Webb, R. H., Bowers, J. E., and Hastings, J. R. (2003). *The Changing Mile Revisited*. Tucson, ARI: University of Arizona Press.

Vesk, P. A., and Westoby, M. (2004). Sprouting ability across diverse disturbances and vegetation types worldwide. *J. Ecol.* 92, 310–320. doi: 10.1111/j.0022-0477.2004.00871.x

Wang, H. H., Wonkka, C. L., Grant, W. E., and Rogers, W. E. (2016). Range expansion of invasive shrubs: implication for crown fire risk in forestlands of the southern USA. *AoB Plants* 8:plw012. doi: 10.1093/aobpla/plw012

Westerling, A. L. (2016). Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philos. Trans. R. Soc. B Biol. Sci.* 371:20150178. doi: 10.1098/rstb.2015.0178

Whittaker, R. H., and Niering, W. A. (1965). Vegetation of the Santa Catalina Mountains. *Ariz. A Gradient Anal. South Slope Ecol.* 46, 429–452. doi: 10.2307/1934875

Whittaker, R. H., and Lowe, C. H. (1984). Vegetation of the santa catalina mountains: community types and dynamics. *Vegetatio* 58, 3–28. doi: 10.2307/40022817

Williams, D. G., and Baruch, Z. (2000). African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biol. Invasions* 2, 123–140.

Wilson, R. C., Narog, M. G., Koonce, A. L., and Corcoran, B. M. (1995). "Postfire regeneration in Arizona's giant saguaro shrub community," in *Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II Proc. RMRS-P-36*, eds G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster (Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station), 424–431.

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Spatio-Temporal Patterns of Joshua Tree Stand Structure and Regeneration Following Mojave Desert Wildfires

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Eastern Joshua tree (*Yucca jaegeriana*) plays a central role in the ecology of the Mojave Desert ecosystem. However, the emergence of invasive grass fire-cycles in the last several decades brings into question Joshua trees' tolerance and resilience to changing fire regimes. This study's objective was to examine the effects of wildfires on the structure and regeneration potential of Joshua trees forests. We examined the density, size class structure, and regeneration response of Joshua tree populations on a network of one kilometer transects along the boundaries of four independent wildfires and the interior of the largest fire that occurred 15 years ago (2005) in the northeast Mojave Desert. Burned edge and burned interior transects had 23- and 4.1-fold lower Joshua tree stand densities than unburned transects. The more robust recovery of stand density along burned interior transects compared to burned edge transects appears to be primarily driven by more prolific vegetative sprouting. Our data show that Joshua trees can sprout vegetatively following fire, but it is not a strong or consistent post-fire resprouter. Limiting the spread of invasive annual grasses and novel fire regimes will be critical to maintaining healthy Joshua tree populations into the future, particularly on the edge of its ecological range.

Keywords: invasive grass fire cycle, Mojave Desert, vegetative regeneration, wildfire, *Yucca* brefifolia

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INTRODUCTION

Wildfire activity is changing across earth's ecosystems due to human activity resulting in novel fire regimes that can have lasting effects on vegetation (Bowman et al., 2009; Crotteau et al., 2013). Wildfires are increasing in deserts of North America, primarily driven by invasive grass fire cycles (Brooks et al., 2004; Balch et al., 2013). Red brome *(Bromus rubens* L.), an invasive annual grass, has played a significant role in increasing fire activity in the Mojave Desert by increasing plant fuels' continuity and flammability upon drying at the end of the growing season (Brooks and Matchett, 2006). Fire risk is especially high in years with early fall precipitation and warm winter temperatures that produces longer growing seasons that fuel red brome growth (Horn et al., 2015; Horn and St. Clair, 2017). There is concern that increasing fire activity in North American deserts may favor the establishment and spread of exotic alien species to the exclusion of the native plant communities (Klinger and Brooks, 2017).

Desert wildfires alter desert plant community composition and function and strongly influence plant community succession (Horn et al., 2015). Plant community recovery following fire varies dramatically between sites depending on a variety of variables, including pre-fire vegetation composition and structure (Minnich, 1995), fire frequency and severity (Klinger and Brooks, 2017), post-fire climate conditions (DeFalco et al., 2010), and patterns of pollination, seed fate, and herbivory in burned desert landscapes (Bowman et al., 2017; Lybbert and St Clair, 2017). Fire chronosequence studies show a high degree of variability in plant communities' response in post-fire environments (Minnich, 1995; Abella, 2009). The biggest concern related to novel fire regimes in deserts is the potential for state and transition changes due to positive responses of invasive annual grasses to post-fire conditions shortening fire return intervals so that native vegetation has little time to recover (Horn and St. Clair, 2017). Recent evidence suggests that both increasing fire frequency and higher burn severity can lead to pathways of dominance by invasive annual grasses and poor post-fire recovery of native vegetation (Klinger and Brooks, 2017).

Successful post-fire re-establishment of native vegetation depends on species resilience to fire primarily driven by fire tolerance and regeneration characteristics (Shryock et al., 2014). Abella (2010) summarized categories of major perennial species that tend to decrease or increase following fire based on these characteristics. At lower burn severity, desert succulents with high water content tend to be less vulnerable to burning, while two dominant Mojave species, *Larrea tridentata* and *Yucca jaegeriana* may escape because of their taller stature (Minnich, 1995). In contrast, annual and perennial grasses, forbs, and drought-deciduous shrubs still tend to be vulnerable to lower severity ground fire because of their short stature and low water content (Minnich, 1995). High burn severity driven by large woody fuel loads connected by continuous fine fuels can result in greater than 80% losses in plant cover (Minnich, 1995; Abella, 2009; Lybbert et al., 2017). A variety of perennial desert shrubs and grasses show the ability to sprout from surviving roots after fire (Abella, 2010). Desert plants that survive or resprout following fire have shown significantly higher flower and seed production (Lybbert et al., 2017; Molinari et al., 2019), but environmental constraints in post-fire environments may limit plant recruitment from seed (Bryant et al., 2012; Bowman et al., 2017). More research is needed on how seed banks influence post-fire plant community succession (Abella et al., 2013).

Eastern Joshua tree (*Yucca* jaegeriana) (Lenz, 2007) is a semi-succulent, arborescent that can exceed 5 m in height and 300 years in age (Gilliland et al., 2006). Few studies have examined the post-fire ecology of Joshua trees. This is surprising considering Joshua trees' central role in the Mojave Desert ecosystem and the dramatic increase in Mojave Desert wildfire in recent decades. Joshua trees can regenerate vegetatively following fire (Loik et al., 2000; Abella, 2010) but are classified as having limited post-fire regeneration potential (Abella, 2009; Shryock et al., 2014). Furthermore, woody shrubs facilitate Joshua tree seedling establishment (Brittingham and Walker, 2000), so reducing shrub cover following fire would impose additional limitations on Joshua tree regeneration. What is more poorly known are spatial patterns of Joshua tree regeneration as a function of distance from burn boundaries where there may be variation in burn effects or differences in the biological community's characteristics. In other forest systems edge effects are known to strongly influence seedling establishment and patterns of recruitment (Montoro Girona et al., 2018; Martin et al., 2020).

Joshua tree forests are common in the northeast Mojave Desert, where fires related to red brome invasion are becoming larger and more frequent (Horn and St. Clair, 2017). Several large and independent fires that occurred in the summer of 2005 in the northeast Mojave provided an opportunity to assess Joshua trees' regeneration in post-fire environments. This study's objective was to characterize the post-fire structure and regeneration of Joshua tree stands 15 years after the 2005 wildfires. We addressed the following questions: (1) What are the characteristics of Joshua tree stands 15 years after wildfire occurrence? (2) Is there evidence of post-fire Joshua tree regeneration, and does it vary spatially between burned edges along fire boundaries to locations deeper into the fire's interior? We hypothesized greater Joshua tree regeneration along burned edges due to higher seed dispersal from adjacent unburned vegetation and lower burn severity.

MATERIALS AND METHODS

Study Area

This study was conducted in the Beaver Dam Wash of southwestern Utah in May 2020. The study area is characterized by native shrubs of which *Coleogyne ramosissima* Torr., *Larrea tridentata* (DC.) Coville, and *Ambrosia dumosa* (A. Gray) Payne

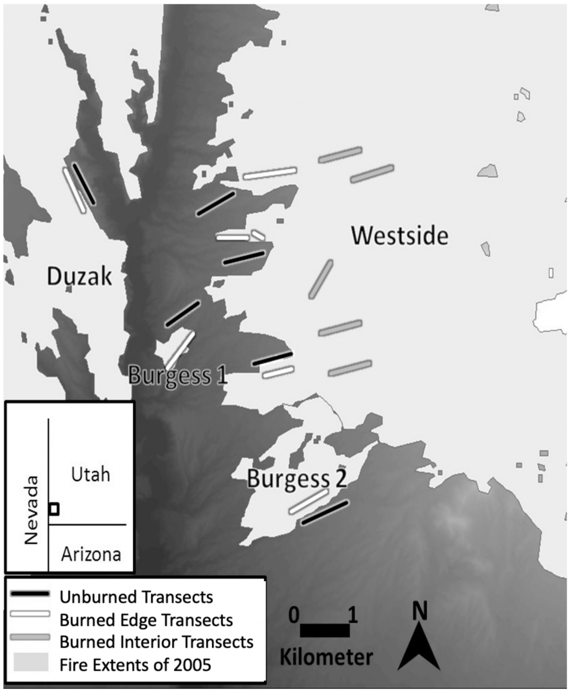

FIGURE 1 | Map of Beaver Dam Wash (N37.14, W114.03) study site. Transect lines in four independent burns that occurred in the summer of 2005 with 1 km long transects along unburned (black), burned edge (white) and burned interior (gray) locations in the landscape. Study area is located in the southwest corner of Utah.

are the most common. Two yucca species are common in the study area *Yucca baccata* Torr. and *Yucca jaegeriana*. Common native herbaceous plants included *Sphaeralcea ambigua* A.Gray spp., *Baileya multiradiata* Harv. & A. Gray, *Astragalus nuttaliianus* DC., *Plantago* spp. (*P. patagonica* and *P. ovata*), and *Descurainia pinnata* (Walter) Britton. Soil in the area is classified as a gravelly sandy loam (Soil Survey Staff, 2015). Mean annual precipitation is 272 mm and mean annual temperature is 16°C (Western Regional Climate Center, 2000). In recent years the landscape has been altered by plant invasions resulting in changing fire regimes characterized by larger and more frequent fires in the Mojave Desert (Brooks et al., 2004; Brooks and Matchett, 2006; Horn and St. Clair, 2017). Invasive annual grasses, *Schismus arabicus* Nees., and *Bromus rubens* L. responded positively to early fall precipitation in 2004 resulted in the build-up of fine fuels that triggered multiple, large-scale fires in the study area (Beaver Dam Wash) in the summer of 2005 (Horn and St. Clair, 2017). Burn transects were placed within four independent fires that occurred during the summer of 2005: Westside (June, 27,059 ha), Duzak (July, 7,065 ha–within Utah), Burgess 1 (July, 60 ha), and Burgess 2 (July, 712 ha) (Utah Bureau of Land Management).

Study Design

We established a network of 1 km long paired transect lines. Six transect pairs were positioned along adjacent burned/unburned boundaries within the four independent fires in 2005 (**Figure 1**). Paired transects were placed in areas where they would be adjacent to one another within 200 m on either side of a burn boundary. For the three transects pairs in the Westside fire we added an additional criterion of spreading them as far apart as possible to get broader coverage of the burned area. A single transect pair was placed in the Burgess 1, Burgess 2, and Duzak fires to get statistical replication in independent fires. The remaining three transects were spread across the Westside fire which was fourfold larger than the Duzak fire and several orders of magnitude larger than the Burgess 1 and 2 fires making up the majority of the area burned during the 2005 fires. Five additional transects were established in the interior of the Westside fire to compare Joshua tree regeneration responses in the interior of burned landscapes compared to adjacent burned edges. All transect pairs were selected on these criteria using GIS mapping software to prevent any bias from choosing sites while on location. We estimated pre-fire Joshua tree stand densities along burned-edge and burned-interior transects by counting the number of Joshua trees in a 100 m^{-2} square area in the center of each transect. Density counts were generated from 2004 image layers of the study area using Google Earth Pro. There were no differences in pre-fire stand density between burned-edge and burned-interior transects ($P = 0.71$) or burn severity (Lybbert et al., 2017).

Measurements

At each 100-increment point along the transect, we measured the distances to the two nearest living Joshua trees on each side of the transect tape to estimate population density. This included surviving trees that had burned partially in the 2005 fires but still had living branches. On each of the trees (20 trees/transect), we measured tree height and trunk diameter. For Joshua trees under 1 m in height that would likely have regenerated after the fire based on sprout growth estimates (Keith, 1982), we measured the distance to the nearest dead Joshua tree. Tree height was determined using a telescoping meter stick. Trunk diameter was measured 20 cm above the soil surface using tree calipers.

Statistical Analysis

Mixed-effects linear models were used to examine the effects of burn condition and location (unburned, burned edge, burned interior) on Joshua tree stand density, tree height, trunk diameter, and percent of sprouts next to dead Joshua trees. In our mixed models, transect type (unburned, burned-edge, burned-interior) and height class were specified as a fixed effect, and site (transect number) was specified as a random effect.

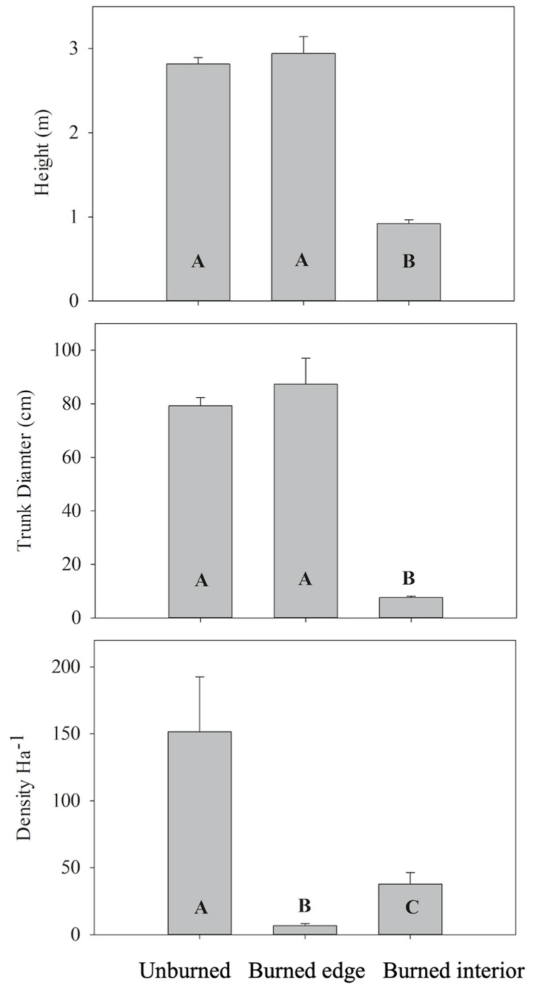

FIGURE 2 | Height, trunk diameter and stand density of living Joshua trees (means ± SE) along unburned, burned edge and burned interior transects. Different letters denote statistically significant difference in mean values ($P < 0.05$) between different burn conditions using Tukey's HSD. $N = 6$ for unburned and burned edges, $N = 5$ for burned interior.

Tukey's LSD was used to test mean differences across burn conditions within each height class. Assumptions of normality and homoscedasticity were visually inspected using residual plots (e.g., histogram, scatterplot, and qqnorm of residuals). To meet equal variance assumptions, data were log-transformed when appropriate. All calculations, models, assumption analyses, and statistical significance determinations were performed using JMP statistical software (version 15).

RESULTS

The average stand density, height, and stem diameter varied significantly between Joshua trees growing along burned interior transects compared to unburned and burned edge transects. Joshua tree stand density was dramatically lower along burned edge (23-fold) and burned interior transects (4.1-fold) compared to unburned transects ($P < 0.0001$) (**Figure 2**). Stand density was sixfold greater along burned interior transects compared to burned edge transects. The average height and trunk diameter of Joshua trees along burned interior transects were approximately 3.2- and 11-fold lower than the height and diameter averages of Joshua tree stands along burned edge and unburned transects ($P < 0.0001$) (**Figure 2**).

Height class distribution varied dramatically between Joshua trees growing along burned interior transects compared to unburned and burned edge transects. Nearly 80% of Joshua trees growing along burned interior transects were less than a meter tall, compared to less than 15% in the same height class for unburned and burned edge transects ($P < 0.0001$) (**Figure 3**). There was no statistical difference in the proportion of Joshua trees in the 1–2 m height class among the three transect types ($P = 0.13$). Unburned and burned edge transects had approximately 6-, 21-, and 5-fold higher proportions of Joshua trees in the 2–3, 3–4, and 4–5 m height classes compared to burned interior transects ($P < 0.0001$) (**Figure 3**). The majority of Joshua trees growing along burned edge and unburned transects were in the 1–4 m height range, with the largest proportion (near 40%) in the 3–4 m height class (**Figure 3**).

There was evidence of vegetative regeneration through root sprouting of Joshua trees, particularly along burned interior transects. Nearly 75% of Joshua trees (<1 m tall) growing along burned interior transects were growing from the base of dead Joshua trees compared to 33% of trees (<1 m tall) next to the base of dead Joshua trees along burned edge transects ($P = 0.0005$) (**Figure 4**). We did not find any young Joshua trees growing in proximity to dead Joshua trees along unburned transects.

DISCUSSION

Our results provide evidence that Joshua tree forests exhibit significant changes in stand structure in post-fire environments depending on fire effects and regeneration responses. Reductions in stand density along burn transects were expected due to fire effects, but contrary to our hypothesis we found four-fold greater Joshua tree density along burned interior transects compared to burned edge transects (**Figure 2**). Minnich (1995) suggested

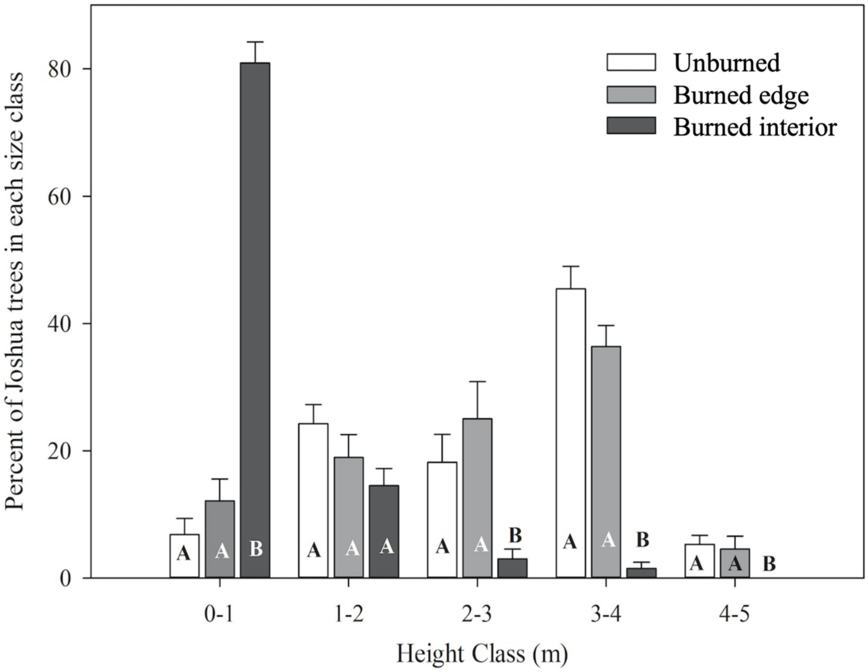

FIGURE 3 | Tree height distribution (means ± SE) of living Joshua trees along unburned, burned edge and burned interior transects. Different letters denote statistically significant difference in mean values ($P < 0.05$) between different burn conditions within each height class using Tukey's HSD. $N = 6$ for unburned and burned edges, $N = 5$ for burned interior.

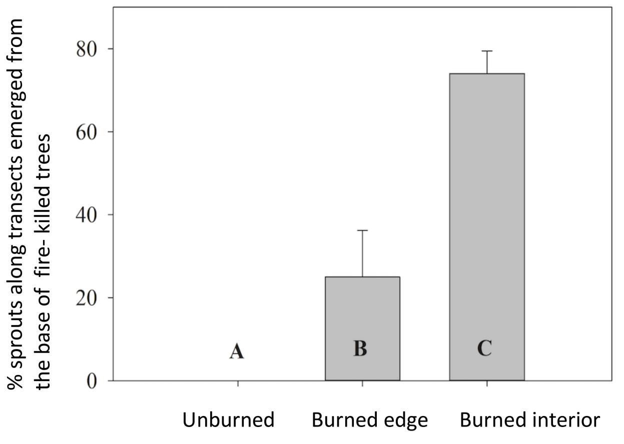

FIGURE 4 | Percent of Joshua tree sprouts (<1 m tall) along transect lines emerged from the base of a burned standing dead or fallen Joshua tree that died in the 2005 fire along unburned, burned edge and burned interior transects (means ± SE). Different letters denote statistically significant difference in mean values ($P < 0.05$) using Tukey's HSD.

that Joshua tree's higher vegetative regeneration could be related to lower burn severity. However, vegetation surveys of post-fire plant community cover and density showed similar burn severity in the burned, interior locations compared to burned edges in an earlier study along these same study transects (Lybbert and St Clair, 2017). Instead, it appears that increases in stands density in burned interiors is driven by significantly higher post-fire sprouting based on our size class analysis (**Figure 3**). This is further supported by the significantly shorter and smaller diameter stand structure of Joshua trees growing along burned interior transects (**Figure 2**).

Joshua trees have been shown to sprout from the root crown of burned Joshua trees the year following a fire (Loik et al., 2000). Joshua trees' average height along burned interior transects was just under 100 cm (**Figure 2**) due to the high proportion of sprouts less than 1 m tall (**Figure 3**). Growth rates of 3.1–3.8 cm/year have been estimated for regenerating Eastern Joshua tree (Gilliland et al., 2006; Esque et al., 2015). Over the 15 years since the fire, this would have resulted in approximately 47–57 cm of vertical growth. This suggests that Joshua trees under 1 meter in height common in the burned interior transects were established soon after the 2005 fires.

There is evidence in the literature of up to 30% of burned Joshua trees resprouting after fire (Loik et al., 2000). Other studies tend to show significantly less post-fire Joshua tree regeneration (Minnich, 1995; Abella, 2010), which may represent differences in post-fire sprouting responses of the Eastern Joshua tree (*Yucca jaegeriana*) compared to the Western Joshua tree (*Yucca brevifolia*). Our study similarly shows a wide range of regeneration responses within a burned desert landscape. In our study, the high proportion of young Joshua trees regenerating in burned interior locations (**Figure 4**) appears to be driven by vegetative sprouting from the base of Joshua trees that burned in the 2005 fire (**Figure 5**). It is unclear why Joshua tree sprouting would have been higher along interior transects than those along burned edges (**Figure 2**). Burned interior transects were higher in elevation but only slightly on average (960 m vs. 1,050 m) and elevation showed no correlation with regeneration density ($R^2 = 0.05$, $P = 0.37$). The literature hints at one possible hypothesis. Both Jackrabbits and gophers are known to eat regenerating Joshua trees, resulting in high mortality rates (DeFalco et al., 2010; Esque et al., 2015). Jackrabbits prefer shrubland habitat typical of the unburned transect lines and utilize burned habitats less (Knick and Dyer, 1997). This could result in lower rates of Joshua tree herbivory along burned interior transects than burned edge transects adjacent to unburned habitat where rabbits may be more active. Additional studies would need to be conducted to test his hypothesis.

FIGURE 5 | Photos taken along burn interior transects in the spring of 2020 showing Joshua tree sprouts emerging from the base of Joshua trees that burned in the 2005 fire.

Our data are consistent with previous studies showing the Joshua tree can sprout vegetatively following fire (Loik et al., 2000), but it is not a strong or consistent post-fire resprouter

(Abella, 2010). The literature indicates that post-fire resprouting constraints on Joshua tree may be compounded by drought events (DeFalco et al., 2010) that are expected to become more frequent in the future (Abatzoglou and Kolden, 2011) and animal herbivory (Esque et al., 2015). Hotter and drier future climates are expected to physiologically contract Joshua tree's current range (Cole et al., 2011; St Clair and Hoines, 2018). In addition, extended and more severe droughts are likely to promote more fire in the Mojave Desert, causing direct mortality of Joshua trees and limiting seedling establishment by burning native nursing shrubs (Brittingham and Walker, 2000). Limiting the spread of invasive annual grasses and novel fire regimes will be critical to maintaining healthy Joshua tree populations into the future, particularly on the edge of its ecological range (Barrows et al., 2020).

CONCLUSION

Our study shows a high degree of variability in post-fire regeneration patterns of Joshua tree based on distance from burn boundaries. Joshua tree, which is thought of as a poor-post fire sprouter, especially under high burn severity (Abella, 2009; Shryock et al., 2014) did show evidence of post-fire sprouting success in our study (**Figure 4**). This seems especially important since we found little evidence of post-fire regeneration of Joshua tree from seed. Surprisingly, regeneration density was higher along interior transects than along burn edges although additional surveys in larger burned areas are needed to validate our findings and conclude that it is a broader geographic phenomenon in the Mojave Desert. However, additional experiments are needed to better identify the factors driving the patterns we observed. For example, monitoring of herbivory and environmental correlates such as soil resource availability and topographical variation that may contribute to variability in Joshua tree resprouting success in post-fire environments.

While we observed Joshua tree vegetative regeneration following high severity fire, regeneration densities were still dramatically lower than typical Joshua tree stands in unburned areas even 15 years after the fire (**Figure 2**). This suggests that post-fire vegetative sprouting alone isn't sufficient to re-establish typical stand densities in the years following fire. Since climate change is likely to increasingly constrain Joshua tree regeneration from seed (Bryant et al., 2012) management approaches that limit the establishment and spread invasive grasses and human ignitions that spread wildfire into Joshua tree stands is of high priority. Where fire does occur and Joshua tree stand re-establishment is desired, outplantings may be a restoration approach to re-establish Joshua tree stands. However, research is needed to explore the viability of this option and even then it would probably only be economically feasible at small spatial scales (Perez et al., 2019).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SeS and ES conducted the field surveys. SeS curated the data. SeS and SaS conceive the study, analyzed the data, and wrote the manuscript. ES reviewed the manuscript and provided feedback. All authors contributed to the article and approved the submitted version.

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REFERENCES

Abatzoglou, J. T., and Kolden, C. A. (2011). Climate change in Western US deserts: potential for increased wildfire and invasive annual grasses. *Rangel. Ecol. Manag.* 64, 471–478. doi: 10.2111/REM-D-09-00151.1

Abella, S. R. (2009). Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. *J. Arid Environ.* 73, 699–707. doi: 10.1016/j.jaridenv.2009.03.003

Abella, S. R. (2010). Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *Int. J. Environ. Res. Public Health* 7, 1248–1284. doi: 10.3390/ijerph7041248

Abella, S. R., Chiquoine, L. P., and Vanier, C. H. (2013). Characterizing soil seed banks and relationships to plant communities. *Plant Ecol.* 214, 703–715. doi: 10.1007/s11258-013-0200-3

Balch, J. K., Bradley, B. A., D'Antonio, C. M., and Gomez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Glob. Change Biol.* 19, 173–183. doi: 10.1111/gcb.12046

Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., et al. (2020). Validating climate-change refugia: empirical bottom-up approaches to support management actions. *Front. Ecol. Environ.* 18:298–306. doi: 10.1002/fee.2205

Bowman, D., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., et al. (2009). Fire in the earth system. *Science* 324, 481–484.

Bowman, T. R. S., McMillan, B. R., and St Clair, S. B. (2017). Rodent herbivory differentially affects mortality rates of 14 native plant species with contrasting life history and growth form traits. *Oecologia* 185, 465–473. doi: 10.1007/s00442-017-3944-y

Brittingham, S., and Walker, L. R. (2000). Facilitation of Yucca brevifolia recruitment by Mojave Desert shrubs. *West. North Am. Nat.* 60, 374–383.

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., et al. (2004). Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.

Brooks, M. L., and Matchett, J. R. (2006). Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. *J. Arid Environ.* 67, 148–164. doi: 10.1016/j.jaridenv.2006.09.027

Bryant, M., Reynolds, J., DeFalco, L. A., and Esque, T. C. (2012). Short seed longevity, variable germination conditions, and infrequent establishment events provide a narrow window for *Yucca brevifolia* (Agavaceae) recruitment. *Am. J. Bot.* 99, 1647–1654. doi: 10.3732/ajb.1200099

Cole, K. L., Ironside, K., Eischeid, J., Garfin, G., Duffy, P. B., and Toney, C. (2011). Past and ongoing shifts in Joshua tree distribution support future modeled range contraction. *Ecol. Appl.* 21, 137–149. doi: 10.1890/09-1800.1

Crotteau, J. S., Varner, J. M. III, and Ritchie, M. W. (2013). Post-fire regeneration across a fire severity gradient in the southern Cascades. *For. Ecol. Manag.* 287, 103–112.

DeFalco, L. A., Esque, T. C., Scoles-Sciulla, S. J., and Rodgers, J. (2010). Desert wildfire and severe drought diminish survivorship of the long-lived Joshua tree (*Yucca Brevifolia*: *Agavaceae*). *Am. J. Bot.* 97, 243–250. doi: 10.3732/ajb.0900032

Esque, T. C., Medica, P. A., Shryock, D. F., DeFalco, L. A., Webb, R. H., and Hunter, R. B. (2015). Direct and indirect effects of environmental variablity of growth and survivorship of pre-reproductive Joshua trees, Yucca brevifolia Englem. (Agavaceae). *Am. J. Bot.* 102, 85–91. doi: 10.3732/ajb.1400257

Gilliland, K. D., Huntly, N. J., and Anderson, J. E. (2006). Age and population structure of Joshua trees (*Yucca brevifolia*) in the northwestern Mojave Desert. *West. North Am. Nat.* 66, 202–208.

Horn, K. J., and St. Clair, S. B. (2017). Wildfire and exotic grass invasion alter plant productivity in response to climate variability in the Mojave Desert. *Landsc. Ecol.* 32, 635–646. doi: 10.1007/s10980-016-0466-7

Horn, K. J., Wilkinson, J., White, S., and St Clair, S. B. (2015). Desert wildfire impacts on plant community function. *Plant Ecol.* 216, 1623–1634. doi: 10.1007/s11258-015-0546-9

Keith, S. (1982). A tree named Joshua. *Am. For.* 88, 40–42.

Klinger, R., and Brooks, M. (2017). Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems. *J. Ecol.* 105, 1521–1533. doi: 10.1111/1365-2745.12863

Knick, S. T., and Dyer, D. L. (1997). Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *J. Wildl. Manag.* 61, 75–85. doi: 10.2307/3802416

Lenz, L. W. (2007). Reassessment of *Yucca brevifolia* and recognition of *Y. jaegeriana* as a distinct species. *Aliso* 24, 97–104. doi: 10.5642/aliso.20072401.07

Loik, M., St. Onge, C., and Rogers, J. (2000). "Post-fire recruitment of *Yucca brevidolia* and *Yucca schidigera* in Joshua Tree National Park, California," in *Second Interface Between Ecology and Land Development in California. Open-File Report 00-62*, eds J. E. Keeley, M. Baer-Keely, and C. J. Fotheringham (Sacramento, CA: U.S. Geological Survey), 79–85.

Lybbert, A. H., and St Clair, S. B. (2017). Wildfire and floral herbivory alter reproduction and pollinator mutualisms of Yuccas and Yucca moths. *J. Plant Ecol.* 10, 851–858. doi: 10.1093/jpe/rtw077

Lybbert, A. H., Taylor, J., DeFranco, A., and St Clair, S. B. (2017). Reproductive success of wind, generalist, and specialist pollinated plant species following wildfire in desert landscapes. *Int. J. Wildl. Fire* 26, 1030–1039. doi: 10.1071/WF16222

Martin, M., Girona, M. M., and Morin, H. (2020). Driving factors of conifer regeneration dynamics in eastern Canadian boreal old-growth forests. *PLoS One* 15:e0230221. doi: 10.1371/journal.pone.0230221

Minnich, R. (1995). "Wildland fire and early postfire succession in Joshua tree woodland and blackbrush scrub of the Mojave Desert of California," in *Ancient Surfaces of the East Mojave Desert*, eds R. E. Reynolds and J. Reynolds (San Bernardino CA: Museum Association Quarterly), 99–106.

Molinari, R. L., Bishop, T. B. B., Bekker, M. F., Kitchen, S. G., Allphin, L., and St Clair, S. B. (2019). Creosote growth rate and reproduction increase in postfire environments. *Ecol. Evol.* 9, 12897–12905. doi: 10.1002/ece3.5771

Montoro Girona, M., Lussier, J. M., Morin, H., and Thiffault, N. (2018). Conifer regeneration after experimental shelterwood and seed-tree treatments in boreal forests: finding silvicultural alternatives. *Front. Plant Sci.* 9:1145. doi: 10.3389/fpls.2018.0114

Perez, D. R., Gonzalez, F., Ceballos, C., Oneto, M., and Aronson, J. (2019). Direct seeding and outplantings in drylands of Argentinean Patagonia: estimated costs, and prospects of large-scale restoration and rehabilitation. *Restor. Ecol.* 27, 1105–1116.

Shryock, D. F., DeFalco, L. A., and Esque, T. C. (2014). Life-history traits predict perennial species response to fire in a desert ecosystem. *Ecol. Evol.* 4, 3046–3059. doi: 10.1002/ece3.1159

Soil Survey Staff (2015). *Web Soil Survey*. Washington, DC: Natural Resources Conservation Service.

St Clair, S. B., and Hoines, J. (2018). Reproductive ecology and stand structure of Joshua tree forests across climate gradients of the Mojave Desert. *PLoS One* 13:e0193248. doi: 10.1371/journal.pone.0193248

Western Regional Climate Center (2000). *Western Regional Climate Center*. Tuweep, ARI: Western Regional Climate Center.

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Interactions Among the Fire, Vegetation, the North American Monsoon and the El Niño-Southern Oscillation in the North American Desert Southwest

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Millennial-scale environmental histories from North American desert southwest (SW) ciénegas were examined with existing time series for the North American Monsoon (NAM) and El Niño, in concert with published long-term records of desert vegetation and climate. The goal was to better understand the relationships among fire, the seasonality of precipitation, effective moisture levels, and vegetation type. It was determined that without sufficient winter precipitation fires are rare in desert SW ecosystems. However, it was also determined that in addition to winter moisture, summer ignitions are critical for fire in southwestern deserts. A relationship between the abundance of woody fuels and charcoal abundance was identified, although further calibration on charcoal production in woody vs. grassy desert settings in necessary to fully understand this interplay. Finally, the impacts of climate change and invasive species were considered, with both likely increasing the frequency of fire in desert ecosystems.

Keywords: ciénega, Mexico, pollen, charcoal, woody plant encroachment

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INTRODUCTION

In the southwestern United States, the role of fire in the ecology and maintenance of many upland ecosystems is well understood due to the availability of dendroecological records. Much less is known about the frequency, role and drivers of fire in low elevation desert environments as a result of the paucity and unsuitability of trees for dendrochronological study. There is no consensus on the role of fire in desert settings; some argue that fires are uncommon in desert ecosystems (Brown and Minnich, 1986; Mack et al., 1996; Felger, 2007), while others suggest that prior to the arrival of Euro-Americans fires were frequent and played a significant role in the maintenance of desert systems (McPherson, 1995; Davis et al., 2002; Turner et al., 2003). This disagreement largely stems from limitations of historical observations and prehistoric fire history data from these ecosystems. The Fire Effects Information System (FEIS) produced by the United States Forest Service (USFS) now provides fire regime estimates using Landfire succession modeling.[1] The input for these models is

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[1] https://landfire.gov

based on Biophysical Settings (BpS) "which represent the vegetation that may have been dominant on the landscape prior to Euro-American settlement and are based on both the current biophysical environment and an approximation of the historical disturbance regime" (Fire Effects Information System, 2021). While the FEIS products give ranges of pre-European fire return intervals for many specific arid-land settings (e.g., Southwest desert grasslands 10–883 years; Sonoran desert shrublands 103–1428 years), the fundamental inputs to the model are not truly known and there is large uncertainty associated with the ranges. If the pre-European fire regimes are not known, we cannot fully understand the current and future drivers. Given that the fire is currently being used as a management tool in desert ecosystems, truly knowing the interplay among the key climatic and ecological variables is critical (e.g., Schussman and Gori, 2004).

With the introduction of invasive plants (e.g., *Bromus tectorum*, cheatgrass) and their modification of fuel structure, the fire regime in desert ecosystems is increasing from historic return intervals (Archer and Predick, 2008). Non-native species are expected to thrive in our current and future CO_2 enriched atmosphere, leaving the native plants at a disadvantage. Having a pre-European baseline for fire history and vegetation composition and density would help assess the impact of these invasive species on the vegetation composition, fuel loads, and fire occurrence.

Bestelmeyer et al. (2018) posit that the transition from grassland to shrubland (hereinafter "woody plant encroachment," WPE) is a significant terrestrial regime shift that is not well understood and will likely accelerate with climate change. They argue that these systems are restorable, but potentially to novel compositions. In both the case of invasive plants changing fuel structure and WPE, having knowledge of the pre-European ecosystem would be valuable for assessments of composition changes and for management and restoration efforts.

Sedimentary records are a well-accepted source of prehistoric ecological data including vegetation change and fire regimes. In the desert, ciénega (wetland) sediments can provide information about pre-European vegetation and fire history. For example, Davis et al. (2002) used ~2000 year old microscopic charcoal record to show that regional fire decreased in the Sonoran Desert ca. 200 years ago with the displacement of native agriculture by Euro-American settlement. In arid settings, sedimentary records from ciénegas may be the only way to get direct evidence of past fire and vegetation regimes.

The objectives of this manuscript include:

- To review and synthesize the available long-term records of desert fire ecology and climate from the North American desert southwest (SW) to assess the climate drivers of fire in this ecosystem.
- To examine new data regarding the history of controls on woody plant encroachment (WPE) as it relates to fuel changes in desert environments.
- To examine a North American Monsoon (NAM) time series in concert with El Niño data, as well as charcoal and pollen time series from southwestern desert sites (Brunelle et al., 2018) to assess the role of the seasonal distribution of moisture on desert fire histories.

SITE DESCRIPTIONS AND METHODS

Climate

The desert SW features scattered spring-fed wetlands known throughout the region as ciénegas (Hendrickson and Minckley, 1985; Minckley et al., 2013; Cole and Cole, 2015). Ciénega form and function is largely driven by groundwater levels, which are in turn driven by recharge from winter precipitation (Flint et al., 2004; Scanlon et al., 2006).

The modern precipitation regime of southwest North America is bimodal (Mock, 1996; Shinker, 2010). Winter precipitation is delivered by midlatitude frontal systems (Mock, 1996; Comrie and Glenn, 1998; Shinker, 2010). Summer precipitation is spatially variable, and arrives as convective thunderstorms from the NAM (Mock, 1996; Adams and Comrie, 1997; Sheppard et al., 2002; Diem and Brown, 2006; Shinker, 2010). The winter component of this bimodal regime includes precipitation anomalies resulting from the status of the El Niño/Southern Oscillation (ENSO) (Ropelewski and Halpert, 1986; Cole and Cook, 1998; Gershunov and Barnett, 1998; Cayan et al., 1999; Dettinger et al., 2000). El Niño is the anomalous warming of the near-surface water off the western coast of South America that initiated about 5000 years ago (Enfield, 1992; Liu et al., 2014). Its atmospheric counterpart is the Southern Oscillation, which is measured by changes in barometric pressure (Wallace and Gutzler, 1981; Enfield, 1992). El Niño years in the instrumental record typically result in higher-than-average winter precipitation in the SW; while strong La Niña years cause lower-than-average winter precipitation and are associated with regional drought (Shinker and Bartlein, 2009).

The NAM is a classic monsoon with a seasonal reversal of wind direction that brings moisture into the SW and Mexico in the summer phase. Higgins et al. (1999) propose that Arizona receives 35% of its annual rainfall from the NAM while New Mexico receives 45%. Barron et al. (2012) summarize a Holocene history of the NAM from several proxy records and suggest that before 8000 cal year BP the extent of the NAM was larger but the strength weaker and at about 6000 cal year BP the spatial extent was more focused and stronger. Stahle et al. (2009) and Jones et al. (2015) present NAM time series that are used here to compare with the existing ciénega time series records (Brunelle et al., 2018).

Site Descriptions

San Bernardino Ciénega (31.3°N; 109.3°W, 1160 m asl; **Figure 1**) (SBNWR) is located near Douglas, Arizona and crosses the United States/Mexico border into northeastern Sonora, Mexico. This site is located in the Sonoran Desert, but near the ecotone of the Chihuahuan Desert grassland (Minckley and Brunelle, 2007; Minckley et al., 2009; Brunelle et al., 2010). Currently the ciénega surface is dry except for a few artificial impoundments and small perennial springs managed by the San Bernardino National Wildlife Refuge in the United States, and private landowners on the Mexican side of the border. The ciénega sediments were sampled stratigraphically from an arroyo (ephemeral stream) cut into a desiccated ciénega deposit profile and an active ciénega surface.

Cloverdale Ciénega is located in the Peloncillo Mountains, Coronado National Forest, New Mexico (31°26.141′N, 108°58.517 W, 1640 m asl; **Figure 1**) (Cloverdale). Cloverdale is in the Chihuahuan desert grassland ecosystem and is situated at the woodland-grassland ecotone (Brunelle et al., 2014). Being near the boundary of woodland and grassland makes this location sensitive to changes in community composition over time. Standing water on Cloverdale is ephemeral, however, the sediments currently stay wetted year-round. The site was cored using a vibracorer on the existing active ciénega surface.

Canelo Hills Ciénega (31°33.833′N, 110°31.711′W, 1,506 m asl; **Figure 1**) (Canelo) is a Nature Conservancy preserve located 17 km southeast of Sonoita, Arizona on the east side of the Canelo Hills. The area is in the footprint of the Sonoran Desert ecosystem. This ciénega is located along a stream channel and the wetland sediments were collected using a vibracorer from the surface of the active ciénega.

Babocamari Ciénega (31°37.901′N, 110°27.178′W, 1,391 m asl; **Figure 1**) (Babocamari) is 20 km southeast of Sonoita, Arizona and located between the Whetstone and Huachuca Mountains. The site is also located in the Sonoran Desert ecosystem. Babocamari is part of an area with active ciénega restoration by local landowners. The site was sampled with the vibracorer near the stream channel in an undisturbed area.

Site information for Laguna Pallcacocha (Ecuador, Moy et al., 2002), El Malpais National Monument, New Mexico (Stahle et al., 2009) and Laguna de Janacatlan (Mexico, Jones et al., 2015) can be found in the respective publications.

Methods

As described above, all ciénegas except SBNWR were cored using the Vibracore system (e.g., Lanesky et al., 1979). As all four sites are previously published, details of the coring, sampling and lab methods can be found in Brunelle et al. (2010, 2014, 2018). The existing literature presents pollen percentage and influx data, charcoal/fire histories, WPE analyses, and pollen preservation indices. Pollen preservation in arid settings is often described as problematic (Hall, 1985). However, previous work (e.g., Brunelle et al., 2018) demonstrates that the changes in pollen preservation over the course of a record actually provide information about moisture conditions on the ciénega as pollen will not preserve well in dry sediments due to exposure to oxygen and subsequent deterioration.

For this manuscript several new data sets were considered including. Additional pollen samples to increase the resolution of the recent portion of the Cloverdale record. These new samples allowed the refinement of the WPE interpretations originally presented in Brunelle et al. (2014). Examination of the influx of encroacher taxa (Brunelle et al., 2014) was also conducted on the three additional ciénega sites to determine if the record from Cloverdale was unique or if the pattern of WPE was consistent across the region. These new data were compared with all existing data to assess the fire-vegetation dynamics on millennial time scales. Second, two datasets examining the NAM were compared with the existing ciénega data including Stahle et al. (2009) and Jones et al. (2015). For the Stahle et al. (2009) July precipitation events >3 SD from the average were plotted to indicate strong NAM events, while with the Jones et al. (2015) the 100 year periodicity was plotted (**Figures 2**, **3**).

A Pearson's correlation analysis was conducted among the ciénegas, ENSO (Moy et al., 2002) and NAM (Jones et al., 2015) time series to extract relationships among the climate forcings and ecological responses (**Table 1**).

RESULTS AND DISCUSSION

Long-Term Records

In order to understand fire regimes in desert ecosystems, it is critical to have a baseline understanding of how all the components of this ecosystem have responded to past climate variations. In this manuscript, the "Results and Discussion" sections are merged since much of the ciénega results have been published previously. Fire frequency is inferred from the sedimentary charcoal records of the ciénegas. The records are divided into five periods based on that overall reconstructed fire frequency. The broad-scale assessment of overall climate conditions for the study area are based on the average pollen preservation ratio calculated from the ciénegas (**Figure 2**). These climate interpretations were then compared with a time series for ENSO (Moy et al., 2002), NAM (Stahle et al., 2009; Jones et al., 2015) and the reconstructed fire history (CHAR). There are some "moderate" (Ratner, 2009) correlations noted (yellow shading, **Table 1**) among the variables. The strongest is 0.67 between preservation and the 530 year periodicity of the NAM and all p-values for the highlighted moderate correlations were <0.05. Both ENSO and fire also correlate well with preservation. The NAM and ENSO likely correlate well with preservation because conditions of high effective moisture are favorable for pollen preservation (needs saturated, anoxic environments with low pH). Other interesting moderate correlations exist among the fire history and three periodicities of the NAM, confirming the proposition that NAM is required as an ignition source in desert fire regimes.

Table 1 does not indicate a correlation between NAM and ENSO, however Jones et al. (2015) suggest a relationship between phases of ENSO and the strength of the NAM after a transition period that occurred ∼4000–3000 cal year BP. This suggestion is consistent with a comparison to the Moy et al. (2002) ENSO data (**Figure 2**) which shows general correspondence between the NAM and ENSO.

∼8000–6000 cal Year BP – No Fire

El Niño/Southern Oscillation Quiescent, No North American Monsoon Time Series Data

From 8000 to 6000 cal year BP ciénega sediment deposition is only active at SBNWR. There is essentially no evidence of fire at SBNWR between 8000 and 6000 cal year BP given that average charcoal accumulation rate (CHAR) was zero during most of this interval. During this time period, the preservation ratio is very

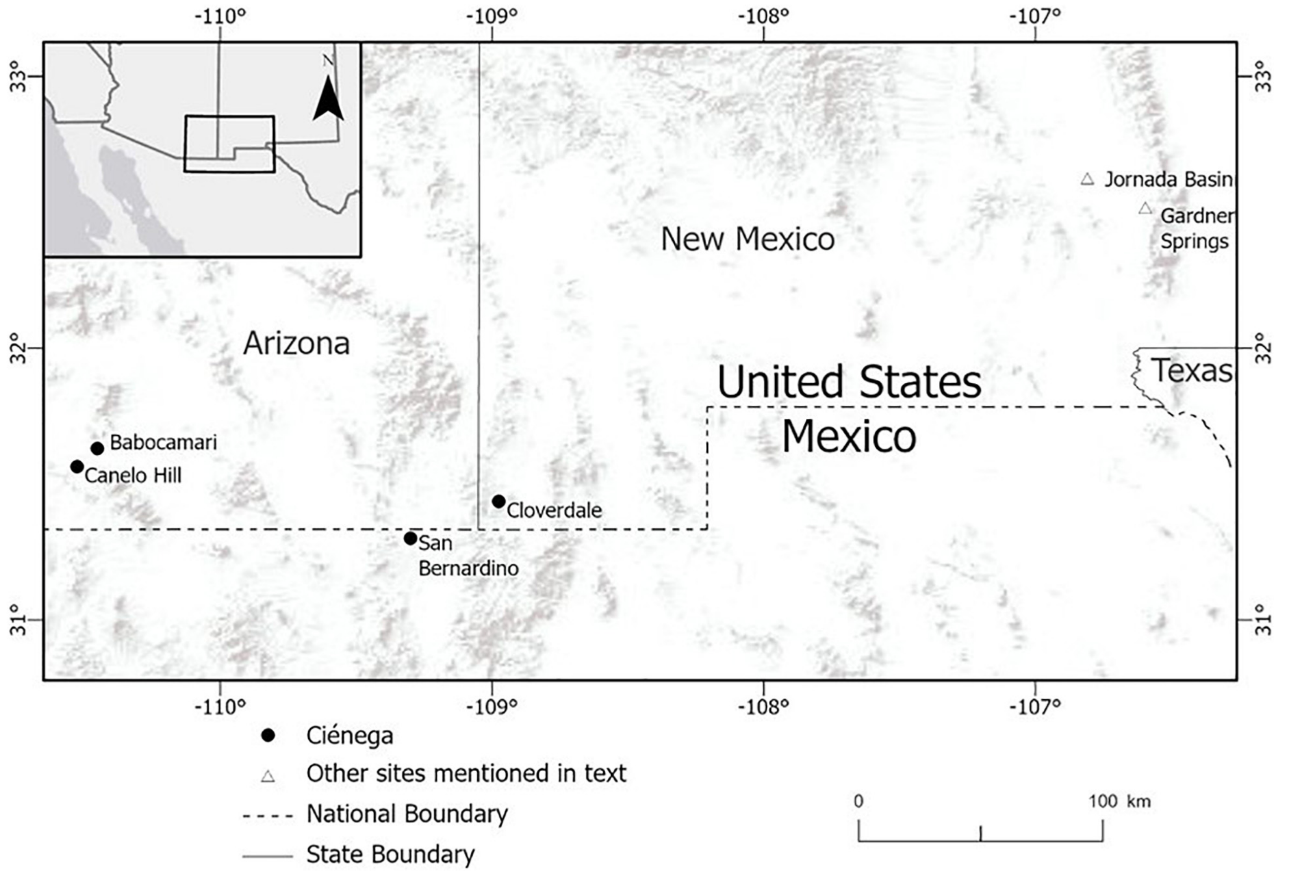

FIGURE 1 | Site map of research sites mentioned in the text.

low (**Figure 2**), indicating that the ciénega was not continuously wetted. This aridity corresponds to a low occurrence of El Niño-like events (i.e., quiescent El Niño) (Moy et al., 2002). Desert wetlands rely on elevated water tables recharged by winter precipitation (Flint et al., 2004; Scanlon et al., 2006). The infrequent El Niño events from 8000 to 6000 cal year BP would have resulted in dry surface conditions at SBNWR.

The Jones et al. (2015) time series does not include this period so a direct comparison could not be made for the Moy et al. (2002) time series. However, Barron et al. (2012) propose the early Holocene NAM would have been widespread but potentially weaker than later in the Holocene. In desert ecosystems the occurrence of fire depends on the presence and continuity of fine fuels to transmit fire (e.g., Brooks and Pyke, 2002). Currently fine fuel production in the desert is associated with winter storms [e.g., desert superblooms (Winkler and Brooks, 2020)] which then provide a continuous fuel source that is prone to drying, which can be readily ignited by lightning during the late-summer NAM season. Tagestad et al. (2016) indicate that most large fires in the Mojave occur when there is a significant summer moisture component (NAM), but without the fine fuels of winter precipitation the occurrence of fire decreases. This early Holocene period of low winter/moderate-high summer precipitation appears to be a non-analog for the modern setting as there is currently no such described Mojave precipitation regime (Tagestad et al., 2016). The early Holocene precipitation and fire regime data from SBNWR suggests that an active NAM is not enough for large desert fires to occur; large fires also require winter moisture to generate fuels.

The influx of taxa linked to WPE were low in the early Holocene and never exceeded 19 grains/cm^2/year (**Figure 2**), while the abundance of dry adapted Amaranthaceae dominated the pollen assemblage (**Figure 4**). These data in concert with the low preservation ratio also suggest overall dry conditions for this period of low fire activity.

Monger (2003) presents a record of climate change for the desert SW in the context of research conducted at the Jornada Long Term Ecological Research (LTER) in the Jornada Basin, New Mexico as well as other long-term records collected from elsewhere around the region. Monger (2003) analyzed $\delta^{13}C$ from paleosols to interpret past vegetation regimes. The $\delta^{13}C$ values were consistent with their recorded increase of Amaranthaceae pollen and erosion that they interpret as a change from a C_4 grassland to a C_3 shrubland between 8000 and 5700 cal year BP. The Monger (2003) record of Amaranthaceae is in agreement with the record from SBNWR, which recorded high Amaranthaceae values during this period. The grass pollen is

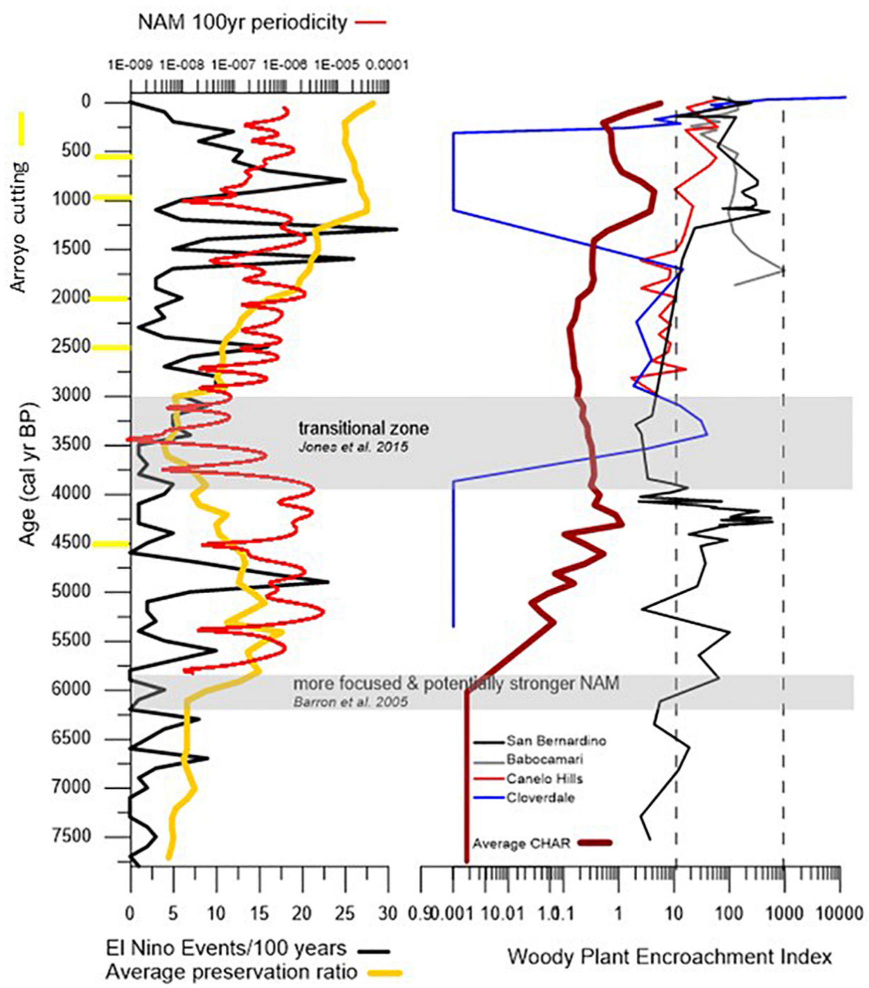

FIGURE 2 | Left panel: Long-term records of El Niño/Southern Oscillation (ENSO) events (black line, Moy et al., 2002), North American Monsoon (NAM) frequency (red line, Jones et al., 2015), average pollen preservation (gold line). Arroyo cutting events are indicated on the y-axis as yellow bars. **Right panel:** average charcoal accumulation rates (CHAR) (dark red line, Brunelle et al., 2018), and woody plant encroachment (WPE) (see color assignments on figure) indices for the four ciénega sites described in the text.

low at SBNWR but C_4/C_3 specificity cannot be determined from palynological data.

~6000–4000 cal Year BP – Increasing Fire Frequency

El Niño/Southern Oscillation Active, North American Monsoon Moderate

During the middle Holocene, average CHAR steadily increases, likely due to continuous fuel production. It is also notable that the beginning of the deposition of wetland sediments at Cloverdale is coincident with a peak in El Niño events and the NAM at ~4750 cal year BP (**Figure 2**). It is likely that enhanced winter and summer precipitation charged the aquifer to the point where standing surface water became common at that site.

The high pollen preservation index (**Figure 2**) also suggests that this time interval was wetter-than-previous. The timing of the preservation index increase is roughly synchronous with the onset of modern ENSO variability (**Figure 2**) and coincides with a stepwise change in charcoal influx in the SBNWR core (Brunelle et al., 2010). Brunelle et al. (2010) propose that the onset of ENSO active (i.e., more frequent El Niño events) led to an increase in fine fuel production (annuals) during spring, which allowed the ignitions by summer convective thunderstorms to carry across the usually sparse desert landscape. The Jones et al. (2015) Ti record of NAM begins at ~6000 cal year BP and shows a moderate level of NAM activity. Barron et al. (2012) identify ~6000 cal year BP as a time of spatially reduced but more intense NAM.

Woody plant encroachment reached the highest of the record at SBNWR with influx values reaching 606 grains/cm^2/year at ~4300 cal year BP. The plant assemblage at SBNWR was dominated by Amaranthaceae but an increase in Asteraceae is evident, which may reflect increased moisture and an increase in fine fuels (**Figure 4A**). Poaceae pollen remains low at SBNWR during the middle Holocene. The WPE at Cloverdale is near zero

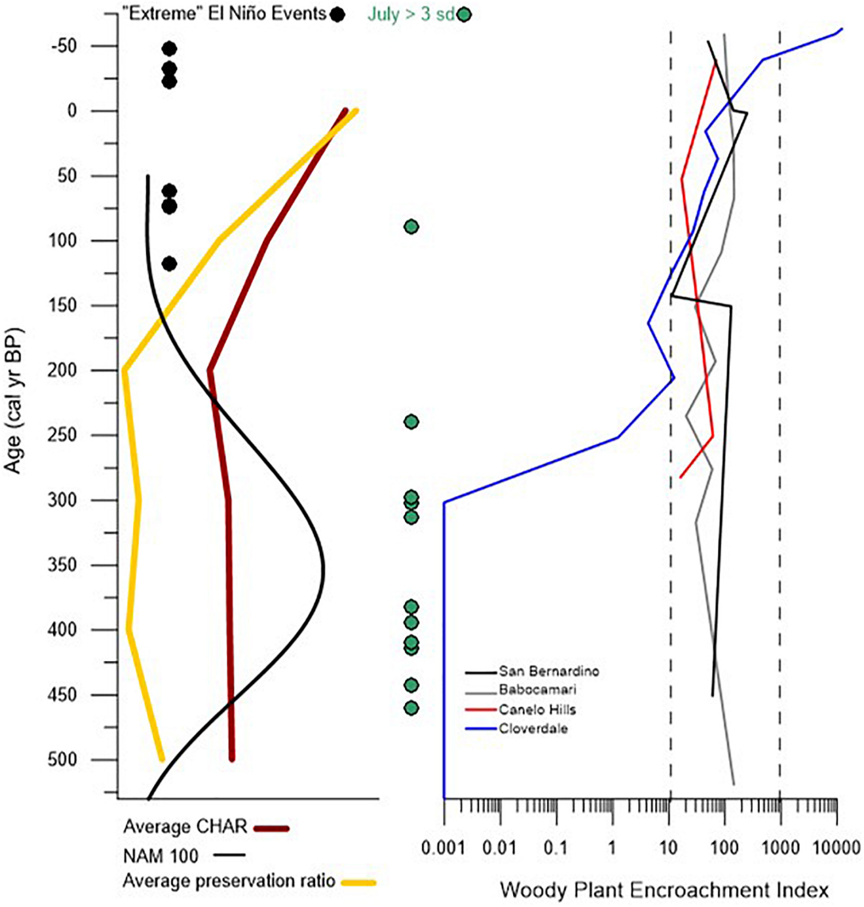

FIGURE 3 | The last ~500 years of the record. **Left panel**: "extreme" El Niño events (black dots) as reported by Brönnimann et al. (2007), and extreme NAM events (green dots, Stahle et al., 2009). Also included are average pollen preservation (gold line) and average CHAR (dark red line, Brunelle et al., 2018). **Right panel**: woody plant encroachment indices (see color assignments on figure) for the four ciénega sites described in the text.

for this entire zone. The dominant taxa at Cloverdale during this time were Asteraceae, Amaranthaceae, and Poaceae (**Figure 4B**).

Monger's (2003) Jornada Basin record also suggests that a wet period occurred between 5700 and 3200 cal year BP. The original pollen record from the desert SW was produced by Freeman (1972) from alluvial sediments in the Chihuahuan desert grassland of southeastern New Mexico. Most pollen records from the desert SW are generated by analyzing either alluvial deposits or packrat middens, which have both provided important information about environmental change over thousands of years. One challenge to interpreting alluvial and packrat midden pollen records is that these records are not continuous. Alluvial deposits are interrupted by cut and fill events, so while pollen information from a stratigraphic layer is valuable and representative for that specific period of time, it is only a discrete snapshot and not a record of continuous change. Packrat midden pollen data have the same issue. In some cases, packrat middens do have stratigraphy, but the depositional environment is still not continuous and uninterrupted sequences not always clearly evident. Dated packrat midden pollen samples again provide a representation of the vegetation at the time the deposit accumulated, but do not provide insight about the drivers of vegetation change through time.

Freeman's (1972) record includes four sampling locations from the Gardner Spring profile. Each profile has one radiocarbon date that constrains the maximum age of the sedimentary section. The oldest sample indicates a transition from scrub to grassland at ~5700–4500 cal year BP. The two ciénega records that capture that time period do not record a similar compositional shift. Cloverdale, which is the closest site to Gardner Springs, shows an increase in grass after ~3500 cal year BP (**Figure 4B**). SBNWR does show a distinct shrubland/grassland transition, but not until ~4000 cal year BP (**Figure 4A**). The Gardner Springs record does not include charcoal data.

Van Devender (1990) indicates, based on packrat midden records, that the Chihuahuan desert scrub developed at ~4500 cal year BP. The SBNWR and Cloverdale pollen records do not show any distinct changes in vegetation at this time, but there are distinct shifts in fire occurrence that align with the onset of ENSO active conditions and an increase in NAM activity. It is likely that the changes Van Devender (1990)

TABLE 1 | Pearson's correlation coefficients (*R*-values).

	PRES	*2*	*20*	*60*	*100*	*170*	*530*	*1850*	*ENSO*	*CHAR*
PRES	1.00									
2	0.02	1.00								
20	0.10	0.31	1.00							
60	−0.03	−0.11	0.24	1.00						
100	0.25	−0.08	−0.02	0.12	1.00					
170	0.15	0.06	0.32	0.07	0.36	1.00				
530	0.67	0.27	0.27	−0.13	0.16	0.41	1.00			
1850	0.45	0.20	0.19	−0.28	0.14	0.33	0.86	1.00		
ENSO	0.38	−0.03	−0.01	−0.12	0.02	0.01	0.29	0.28	1.00	
CHAR	0.59	−0.16	−0.11	−0.14	0.33	0.00	0.30	0.35	0.19	1.00

PRES, average preservation ratio; numbered rows refer to that NAM periodicity as identified from Jones et al. (2015); ENSO, Moy et al. (2002) time series; CHAR, average charcoal accumulation rate from the ciénega sites as a representation of fire history. Yellow highlighting indicates "moderate" correlations per Ratner (2009) and all highlighted values have p-values < 0.05.

identified are also linked to changes in ENSO and the NAM.

Van Devender (1995) also suggests that the middle Holocene desert grassland was likely mesic, not dry as suggested by Antevs (1955). Van Devender's assertion is well supported by a wet period in both ciénega reconstructions that capture the middle Holocene (SBNWR and Cloverdale). Both SBNWR and Cloverdale pollen preservation was elevated from ∼6000 to 4000 cal year BP, indicating wet conditions on both ciénegas.

∼4000 to 2250 cal Year BP – Stable Fire Activity

El Niño/Southern Oscillation Low, North American Monsoon Variable

The ciénega records indicate that fire activity (CHAR) remains stable in this zone despite a transition back to drier-than-previous conditions from ∼4000 to 2250 cal year BP. The interpretation of dryness is based on the dramatic decrease in the pollen preservation index (**Figure 2**). Starting around 4500 cal year BP the number of El Niño events decreased until about 3500 cal year BP. Part of this period is also identified as a "transition zone" by Jones et al. (2015) with respect to the record of the NAM due to the distinctly lower activity (**Figure 2**). It does start high at the beginning of this zone (∼4000 cal year BP) but declines quickly to its lowest of this period by about 3500 cal year BP, after which it steadily increases. It is likely that the decrease in El Niño events, which deliver winter precipitation to the desert SW, and the NAM which provides a summer moisture source, were

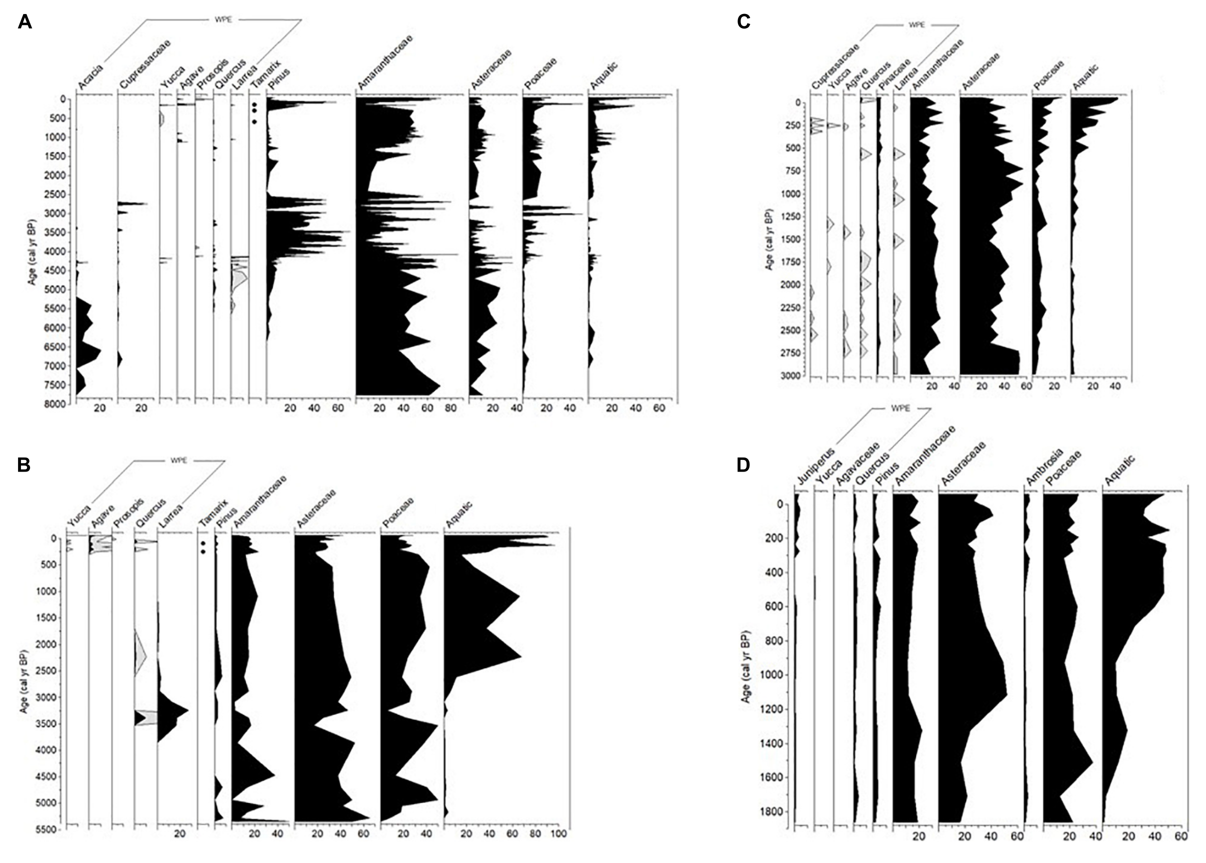

FIGURE 4 | Pollen diagrams from **(A)** SBNWR, **(B)** Cloverdale, **(C)** Canelo Hills, and **(D)** Babocamari. Shaded curves are 10X exaggeration. Full diagrams available in Brunelle et al. (2018).

drivers in shifting the hydroclimate regime to an overall drier state during the ∼4000–2250 cal year BP time period.

Although already low, the WPE at both SBNWR and Cloverdale decreased slightly during this time period. The Canelo Hills ciénega initiates at about 3000 cal year BP during the increase in El Niño events (**Figure 2**) likely due to enhanced water table recharge and the persistent surpluses of surface water at that site. Grasses become more abundant during this time which is most evident from SBNWR (**Figure 4A**).

There seems to be regional agreement among the ciénega reconstructions and other longer-term records from nearby sites. Monger's (2003) Jornada Basin record suggests that a dry period occurred from 3200 to 1500 cal year BP. While this interval does not perfectly align with the ciénega records, given the discontinuous nature of the Jornada Basin record it is likely that the sites mirror the prevailing climate history for the desert SW region. Van Devender (1995) identifies the oldest creosote (*Larrea* spp.) from a packrat midden deposit dating to 3650 cal year BP. Based on the pollen records presented here, the oldest creosote pollen dates are 3524 cal year BP (Cloverdale Ciénega) and 4171 cal year BP (SBNWR), which is consistent with Van Devender's estimation.

Studying periods of arroyo cutting is another way to get prehistoric desert SW climate information (Waters and Haynes, 2001). Waters and Haynes (2001) state that the cause for arroyo cutting is still debated, however, their data suggest that the arroyo cutting prior to Euro-American land modification largely occurred during dry-to-wet transitions. The decreased precipitation associated with dry climate intervals caused water tables to lower and vegetative cover to decrease. The loss of vegetation to anchor soils enhances vulnerability to erosion. As a dry climate interval transitions to a wet period, intense precipitation events, such as those typical of a monsoonal thunderstorm, will readily mobilize the unbound soil causing rapid erosion and arroyo entrenchment. Comparing the arroyo cutting record with the Moy et al. (2002) time series of El Niño events and the Jones et al. (2015) NAM time series supports the argument that arroyo formation is triggered by shifts from dry to wet conditions. **Figure 2** shows five of the six synchronous arroyo cutting events identified by Waters and Haynes (2001) (yellow bars). In nearly every case both the ENSO and NAM time series show a shift from dry to wet conditions.

∼2250 cal Year BP to ∼1500 AD (500 cal Year BP) – Increasing Fire Activity

El Niño/Southern Oscillation and North American Monsoon Increasing

Average CHAR remains high with an increase starting at about 1250 cal year BP. Rising CHAR is probably the result of more frequent El Niño episodes and subsequent periods of fine fuel production. Based on the return to a high preservation ratio (**Figure 2**), the period ∼2250–500 cal year BP is identified as generally wet. Enhanced moisture corresponds well with periods of very frequent El Niño events as recorded by Moy et al. (2002) and an overall increase in NAM activity reported by Jones et al. (2015; **Figure 2**).

Like Cloverdale and Canelo, the Babocamari ciénega initiates during a peak in the number of El Niño events, again likely due to the elevated water table that allows for the existence of surface water. At SBNWR WPE increases slightly, Cloverdale records no WPE, Canelo's WPE is stable, and WPE at Babocamari starts relatively high (∼1,000 grains/cm^2/year) but decreases toward present. The high level of WPE at the onset of the Babocamari record might suggest landcover conversion from a shrub dominated- to a ciénega-dominated system. This conversion can be seen in **Figure 4D** with the marked increase in aquatic taxa. Poaceae pollen remains high or increases during this zone. Monger's (2003) Jornada Basin record indicates a return to more mesic conditions from ∼1500 cal year BP to 1850 AD, however, Freeman (1972) proposes a dry period at ∼2300 cal year BP, from Gardner Springs. Again, while not perfectly aligned with the sediment core records, these overall shifts are fairly consistent across the SW.

500 cal Year BP (1500 AD) to Modern – Increasing Fire Activity

El Niño/Southern Oscillation Decreasing, North American Monsoon Stable

This zone is treated separately because of the influence of Euro-Americans on the desert ecosystem that began around 1500 AD when they arrived in the SW (Hill et al., 2004). The CHAR is relatively low at the start of this zone, but increases toward present, with an inflection at ∼200 cal year BP (1750 AD) (**Figure 3**). Like CHAR, the preservation is relatively low at the start of this zone, but increases toward present, also with an inflection at ∼200 cal year BP (1750 AD). The 1750 AD inflection (**Figure 3**) also coincides with the only El Niño events identified as "extreme" for the entire 500-year period (Brönnimann et al., 2007). Increases in snowpack would facilitate both the saturation of the ciénega systems from a higher water table and the production of fine fuels following wet winters.

To add additional data, the 2200 year long July precipitation reconstruction from Stahle et al. (2009) was used identify extreme July precipitation events as a reconstruction of the NAM. The strong correspondence of extreme July precipitation events (Stahle et al., 2009) and high NAM activity (Jones et al., 2015) serves to validate both records. It is also interesting that over the last 500 years the majority of extreme July precipitation events occur between ∼500 and ∼250 years ago; while the extreme El Niño events are all occur in the last 125 years (Brönnimann et al., 2007). CHAR is stable during the period of large July precipitation events, but increases when there are more extreme El Niño events supporting the assertion that fine fuel production from winter precipitation is a critical driver of desert fire.

Average CHAR and pollen preservation trends essentially mirror the WPE from the Cloverdale site, exhibiting a relationship between desert fire and woody fuels at this site. WPE has also increased since 1750 AD, representing a change from fine (grasses) to coarse (woody plants) fuels. The WPE at Babocamari also increases slightly, but at SBNWR and Canelo it remains fairly constant. The more distinct change in WPE at Cloverdale may be the artifact of its location within the Chihuahuan desert grassland bioregion, as opposed to the Sonoran Desert classification of the other sites. The difference in these desert systems may shape their sensitivity to environmental changes, or a sensitivity to recording them, or both.

The pollen data of aquatic taxa from the Canelo and Babocamari pollen records from 1500 AD to modern increase distinctly beginning around 1250 AD (700 cal year BP) (**Figures 4C,D**). This upward trend likely reflects the formation and expansion of the ciénega systems. Functional ciénegas are known to support continued ciénega development by the wetland plants slowing flood pulses and causing the flood water to drop sediment. Over time this process will cause an increase in the spatial footprint of the ciénega system. SBNWR and Cloverdale pollen data indicate an increase in aquatic taxa starting about 1700 AD (250 cal year BP). WPE also increases at this time at Cloverdale, indicating that despite the encroachment of woody plants around the ciénega, the wetted ciénega surface was stable enough to deter woody plants from establishing on the wetland itself.

The WPE was closely examined in Brunelle et al. (2014) to try and isolate the triggers for the encroachment. Brunelle et al. (2014) examined six different possible mechanisms for WPE including (1) natural variability, (2) drought, (3) ENSO, (4) changes in CO_2 concentrations, (5) changes in fire regime and (6) introduction of grazing. They were able to rule out all but increases in CO_2 concentrations and grazing, which is consistent with other assessments. For example, Monger (2003) puts forward grazing and climate as possible drivers of WPE. Monger (2003) subsequently eliminated climate based on Conley et al. (1992). A higher-resolution analysis of the Cloverdale WPE data now demonstrates that CO_2 can likely be eliminated as the main cause of WPE at this site because the increase in CO_2 follows the increase in WPE. Grazing stands out as the main driver of WPE at Cloverdale. Although not the direct cause of WPE, increased CO_2 can create a multiplier effect.

DRIVERS OF FIRE AND CONCLUSION

Paleoenvironmental records are well suited to contribute on the topic of this special volume, "Fire Regimes in Desert Ecosystems: Drivers, Impacts and Changes." Ciénega sediment records of past environments are long and continuous, containing information on fire regimes, changes in vegetation type and abundance, and climate dynamics including the seasonality and relative abundance of precipitation on millennial time scales. Drivers of fire regime in the desert SW include prevailing climate conditions, vegetation type, and vegetation density. In the desert, WPE into areas that were only sparsely vegetated or dominated by grasses will also alter fire regime – which is also extractable from a sedimentary pollen record. The first continuous record of fire from the desert SW (SBNWR) demonstrated that if there are no El Niño events (e.g., before ∼4500 cal year BP) then there is essentially no fire (**Figure 2**; Figure 4 in Brunelle et al., 2010). This relationship between fire occurrence and ENSO conditions indicates that a fundamental control on desert fire regimes is the abundance of winter precipitation, which over the long-term, has controlled the production of the fine, continuous fuels needed to carry fire in the desert. It is compelling that not only the baseline of fire occurrence is driven by ENSO being active, variations in fire regime reflect more quiescent or active periods of ENSO as well.

There is not a single time series that compares the activity or strength of NAM with fire history over long time periods. However, it is known that currently most desert fires occur when there is a significant amount of summer precipitation (Tagestad et al., 2016). It is also well known that lightning generated from monsoonal storms provides the ignition source needed for desert fire. This manuscript presents the ciénega reconstructions of fire and vegetation in concert with two millennial scale reconstructions of NAM. The main conclusions that can be drawn from these data is that the NAM and El Niño events appear to follow similar trends in highs and lows (**Figure 2**) and both are needed to support desert fire. Given the availability of the ciénega cores presented here, a next step in understanding more about past NAM variability would be to extract the Ti record from these other desert sites for more, local time series. It would also be valuable to explore the possible additive effect of ENSO + NAM on charcoal abundance (fire) over time.

Each ciénega record also provides a record of vegetation changes (**Figure 4**). Overall, the ciénega records were consistent with other records of vegetation from the desert SW, e.g., the correspondence among the ciénega records and those from the Jornada Basin site (Monger, 2003). From the pollen time series, an index of WPE was also extracted to specifically examine the history of changes in the abundance of woody plants at each ciénega site with the fire history data (**Figure 2**). Based on the WPE and average CHAR time series, there is a relationship between woody fuels and charcoal abundance (**Figure 2**). This is likely a result of woody fuels leaving greater charcoal evidence (less complete combustion than grasses). If we look at the Fire Effects Information System (2021) data for SW desert grasslands vs. Sonoran shrublands, grasslands have a shorter fire return interval. The influence of fuel type on the average CHAR may be minimized by the fact that shrublands burn less frequently but produce more charcoal, where grassland burn more often with less charcoal produced. It would be a valuable calibration study to assess this quantitatively.

Finally, there is the modern issue of invasive plants in the desert SW. Paleoecological records can detect the arrival of some invasive plants (e.g., *Tamarix*, see **Figure 4**), but one invasive that cannot be detected using currently available palynological methods are non-native grasses. Grass pollen (family Poaceae) is only identifiable to the family taxonomic level, with the notable exception of maize (*Zea mays*). Higher taxonomic specificity in the grass family can be attained with phytolith analyses. It may be valuable to develop some phytolith records from the desert SW to get information on grass diversity beyond the historical record. There are several invasive grasses established in the desert SW, including both annuals and perennials. For example, some annual invasive species include cheatgrass (*Bromus tectorum*), red brome (*Bromus rubens*), and medusahead (Taeniatherum *caput-medusae*), and some perennials such as buffelgrass (*Pennisetum ciliare*), natal grass (*Melinus repens*) and Lehmann lovegrass (*Eragrostis lehmanniana*) (Brooks and Pyke, 2002). These non-native, invasive grasses are changing the fuel situation in desert SW ecosystems by creating an annual, connected fuel source. Many of these grasses were deliberately introduced. For example, buffelgrass was intentionally and widely broadcast in the 1930s as potential forage for grazing cattle. Buffelgrass is drought tolerant and not reliant on El Niño events to germinate and produce fine fuels. It is likely that invasive species, like buffelgrass and others, will mimic El Niño-driven fuel conditions and lead to increased fire in desert ecosystems. This novel component in desert fire ecology certainly leads to new challenges in land and fire management, and will change the fundamental fire regime of the desert unless the spread of buffelgrass and other invasive species is brought under control.

El Niño/Southern Oscillation is a critical driver of desert SW fire regimes and it is important to consider its behavior in the future. The model forecasts are not completely consistent but seem to favor an increase in El Niño events. Capotondi et al. (2020) indicate that the last two decades have seen more El Niño events than any other time on record. Capotondi et al. (2020) is consistent with predictions by Cai et al. (2015) that ENSO events (both El Niño and La Niña) would increase in strength and frequency with intensified surface warming in the southern Pacific Ocean. Importantly, Capotondi et al. (2020) also state that current research is still investigating the relationship between this increased frequency and climate change. Stronger and/or more frequent El Niño events would certainly facilitate the occurrence of desert fire.

The ignition source provided by the NAM is also critical to the occurrence of desert fire so the NAM under climate change conditions also needs to be considered. van der Wiel et al. (2016) suggested that in a 2 X CO_2 environment that there would be no changes in extreme precipitation events associated with the NAM. However, later work by Pascale et al. (2017) indicates a significant decrease in NAM driven summer precipitation. They indicate that this decrease is a result of uniform sea surface warming causing increased atmospheric stability and thus less convection. Pascale et al. (2018) also suggest the amounts of mean summer time rainfall will decrease in a 2 X CO_2 setting, but the possibility of extreme events will increase. Adaptation measures are suggested to deal with the decrease in monsoonal rainfall and the possibility of more severe rainfall events (Pascale et al., 2017, 2018).

Millennial-scale records of fire, vegetation and climate regimes provide a perspective on desert SW fire regimes prior to the influence of Euro-Americans. While this information is certainly helpful in understanding the fundamental drivers of desert SW fire, the basic components of the desert fire regime are changing. With the modern changes in climate, including warming, drying and changes in ENSO and NAM, along with the spread of invasive grasses like buffelgrass we will need to continue to study past, present and future drivers of fire in the desert SW.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are publicly available. These data can be found here: https://doi.org/10.21233/JMWD-YJ04, 067C-HQ21, 1Z1S-GX38, 3A17-2216, and RKTY-2H81.

AUTHOR CONTRIBUTIONS

The author solely conducted the new analyses and wrote the manuscript. The previously published work includes efforts by many other colleagues but are cited as such throughout the text.

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REFERENCES

Adams, D. K., and Comrie, A. C. (1997). The North American monsoon. *Bull. Am. Meteorol. Soc.* 78, 2197–2213.

Antevs, E. (1955). Geologic-climatic dating in the West. *Am. Antiq.* 20, 317–335. doi: 10.2307/277066

Archer, S. R., and Predick, K. I. (2008). Climate change and ecosystems of the southwestern United States. *Rangelands* 30, 23–28. doi: 10.2111/1551-501x(2008)30[23:ccaeot]2.0.co;2

Barron, J. A., Metcalfe, S. E., and Addison, J. A. (2012). Response of the North American monsoon to regional changes in ocean surface temperature. *Paleoceanography* 27:A3206. doi: 10.1098/rstb.2007.0037

Bestelmeyer, B. T., Peters, D. P. S., Archer, S. R., Browning, D. M., Okin, G. S., Schooley, R. L., et al. (2018). The grassland–shrubland regime shift in the southwestern United States: misconceptions and their implications for management. *Bioscience* 68, 678–690.

Brönnimann, S., Xoplaki, E., Casty, C., Pauling, A., and Luterbacher, J. (2007). ENSO influence on Europe during the last centuries. *Clim. Dyn.* 28, 181–197.

Brooks, M.L., and Pyke, D.A. (2002). "Invasive plants and fire in the deserts of North America", in *Proceedings of the Invasive Plant Workshop: The Role of Fire in the Control and Spread of Invasive Species*, eds K. E. M. Galley, T. P. Wilson (Tallahassee: Tall Timbers Research Station). 1–14.

Brown, D. E., and Minnich, R. A. (1986). Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *Am. Midl. Nat.* 116, 411–422. doi: 10.2307/2425750

Brunelle, A., Minckley, T. A., Blissett, S., Cobabe, S. K., and Guzman, B. L. (2010). A∼ 8000 year fire history from an Arizona/Sonora borderland ciénega. *J. Arid Environ.* 74, 475–481. doi: 10.1016/j.jaridenv.2009.10.006

Brunelle, A., Minckley, T. A., Delgadillo, J., and Blissett, S. (2014). A long-term perspective on woody plant encroachment in the desert southwest, New M exico, USA. *J. Veg. Sci.* 25, 829–838. doi: 10.1111/jvs.12125

Brunelle, A., Minckley, T. A., Shinker, J. J., and Heyer, J. (2018). Filling a geographical gap: new paleoecological reconstructions from the desert Southwest, USA. *Front. Earth Sci.* 6:106. doi: 10.3389/feart.2018.00106

Cai, W., Santoso, A., Wang, G., Yeh, S. W., An, S. I., Cobb, K. M., et al. (2015). ENSO and greenhouse warming. *Nat. Clim. Chang.* 5, 849–859. doi: 10.1126/science.1104666

Capotondi, A., Deser, C., Phillips, A. S., Okumura, Y., and Larson, S. M. (2020). ENSO and Pacific Decadal Variability in the Community Earth System Model Version 2. *J. Adv. Model. Earth Syst.* 12:e2019MS002022.

Cayan, D. R., Redmond, K. T., and Riddle, L. G. (1999). ENSO and Hydrologic Extremes in the Western United States. *J. Clim.* 12, 2881–2893. doi: 10.1175/1520-0442(1999)012<2881:eaheit>2.0.co;2

Cole, A., and Cole, C. (2015). An overview of aridland ciénagas, with proposals for their classification, restoration and preservation. *New Mexico Bot.* 28–56.

Cole, J. E., and Cook, E. R. (1998). The changing relationship between ENSO variability and moisture balance in the continental United States. *Geophy. Res. Lett.* 25, 4529–4532.

Comrie, A. C., and Glenn, E. C. (1998). Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. *Clim. Res.* 10, 201–215. doi: 10.3354/cr010201

Conley, W., Conley, M. R., and Karl, T. R. (1992). A computational study of episodic events and historical context in long-term ecological processes: climate and grazing in the northern Chihuahuan desert. *Coenoses* 7, 55–60.

Davis, O. K., Minckley, T., Moutoux, T., Jull, T., and Kalin, B. (2002). The transformation of Sonoran Desert wetlands following the historic decrease of burning. *J. Arid Environ.* 50, 393–412. doi: 10.1006/jare.2001.0914

Dettinger, M. D., Cayan, D. R., Mccabe, G. M., and Marengo, J. A. (2000). "Multiscale streamflow variability associated with El Niño/Southern Oscillation," in *El Niño and the Southern Oscillation-Multiscale Variability and Global and Regional Impacts*, eds H. F. Diaz and V. Markgraf (Cambridge: Cambridge University Press), 113–146. doi: 10.1017/cbo9780511573125.005

Diem, J. E., and Brown, D. P. (2006). Tropospheric moisture and monsoonal rainfall over the southwestern United States. *J. Geophys. Res.* 111:D16112. doi: 10.1029/2005JD006836

Enfield, D. B. (1992). "El Nino Historical and Paleoclimatic Aspects of the Southern Oscillation," in *El Nino: Historical and Paleoclimatic Aspects of the Southern Oscillation*, eds H. F. Diaz and V. Markgraf (Cambridge: Cambridge University Press), 95–117.

Felger, R. S. (2007). "Living resources at the center of the Sonoran Desert: Native American plant and animal utilization," in *Dry Borders: Great Natural Reserves of the Sonoran Desert*, eds Felger and B. Broyles (Salt Lake City: University of Utah Press), 147–192.

Fire Effects Information System [FEIS] (2021). *Fire Effects Information System.* Available online at: https://www.feis-crs.org/feis/ (Accessed June 28, 2021).

Flint, A. L., Flint, L. E., and Hevesi, J. A. (2004). "Fundamental concepts of recharge in the desert southwest: a regional modeling perspective," in *Groundwater Recharge in a Desert Environment: The Southwestern United States*, eds J. F. Hogan, F. M. Phillips, and B. R. Scanlon (Washington: American Geophysical Union), 9. doi: 10.1142/9789811213380_0002

Freeman, C. E. (1972). Pollen study of some Holocene alluvial deposits in Dona Ana County, southern New Mexico. *Tex. J. Sci.* 24, 203–220.

Gershunov, A., and Barnett, T. P. (1998). ENSO Influence on Intraseasonal Extreme Rainfall and Temperature Frequencies in the Contiguous United States: observations and Model Results. *J. Clim.* 11, 1575–1586. doi: 10.1175/1520-0442(1998)011<1575:eioier>2.0.co;2

Hall, S. A. (1985). "Quaternary Pollen Analysis and Vegetational History of the Southwest," in *Pollen Records of Late-Quaternary North American Sediments*, eds V. M. Bryant Jr. and R. G. Holloway (Texas: American Association of Stratigraphic Palynologists Foundation). doi: 10.1111/j.1469-8137.1995.tb04325.x

Hendrickson, D. A., and Minckley, W. L. (1985). Cienegas-vanishing climax communities of the American Southwest. *Desert Plants* 6, 131–175.

Higgins, R. W., Chen, Y., and Douglas, A. V. (1999). Interannual variability of the North American warm season precipitation regime. *J. Clim.* 12, 653–680. doi: 10.1175/1520-0442(1999)012<0653:ivotna>2.0.co;2

Hill, J. B., Clark, J. J., Doelle, W. H., and Lyons, P. D. (2004). Prehistoric demography in the Southwest: migration, coalescence, and Hohokam population decline. *Am. Antiq.* 69, 689–716. doi: 10.2307/4128444

Jones, M. D., Metcalfe, S. E., Davies, S. J., and Noren, A. (2015). Late Holocene climate reorganisation and the north American monsoon. *Quat. Sci. Rev.* 124, 290–295.

Lanesky, D., Logan, B., Brown, R., and Hine, A. (1979). A new approach to portable vibracoring underwater and on land. *J. Sediment. Res.* 49, 654–657.

Liu, Z., Lu, Z., Wen, X., Otto-Bliesner, B. L., Timmermann, A., and Cobb, K. M. (2014). Evolution and forcing mechanisms of El Niño over the past 21,000 years. *Nature* 515, 550–553. doi: 10.1038/ncomms4701

Mack, F., Hoffstadt, J., Esser, G., and Goldammer, J. G. (1996). "Modeling the influence of vegetation fires on the global carbon cycle," in *Biomass Burning and Global Change*, ed. J. S. Levine (Cambridge: The MIT Press), 149–159.

McPherson, G. R. (1995). "The role of fire in the desert grasslands," in *The desert grassland*, eds M. P. McClaran and T. R. van Devender (Tucson: University of Arizona Press), 130–151.

Minckley, T. A., and Brunelle, A. (2007). Paleohydrology and growth of a desert cienega. *J. Arid Environ.* 69, 420–431. doi: 10.1016/j.jaridenv.2006.10.014

Minckley, T. A., Clementz, M., Brunelle, A., and Klopfenstein, G. A. (2009). Isotopic analysis of wetland development in the american southwest. *Holocene* 19, 737–744. doi: 10.1177/0959683609105297

Minckley, T. A., Turner, D. S., and Weinstein, S. R. (2013). The relevance of wetland conservation in arid regions: a re-examination of vanishing communities in the American Southwest. *J. Arid Environ.* 88, 213–221. doi: 10.1016/j.jaridenv.2012.09.001

Mock, C. J. (1996). Climatic controls and spatial variations of precipitation in the western United States. *J. Clim.* 9, 1111–1125. doi: 10.1175/1520-0442(1996)009<1111:ccasvo>2.0.co;2

Monger, H. C. (2003). "Millennial-scale climate variability and ecosystem resonse at the Jornada LTER site," in *Climate Variability and Ecosystem Respoinse at Long-Term Ecological Research Sites*, eds D. Greenland, D. G. Goodin, and R. C. Smith (Oxford: Oxford University Press), 341–369.

Moy, C. M., Seltzer, G. O., Rodbell, D. T., and Anderson, D. M. (2002). Variability of el nino/southern oscillation activity at millennial timescales during the holocene epoch. *Nature* 420, 162–165. doi: 10.1038/nature01194

Pascale, S., Boos, W. R., Bordoni, S., Delworth, T. L., Kapnick, S. B., Murakami, H., et al. (2017). Weakening of the North American monsoon with global warming. *Nat. Clim. Chang.* 7, 806–812. doi: 10.1038/nclimate3412

Pascale, S., Kapnick, S. B., Bordoni, S., and Delworth, T. L. (2018). The influence of CO2 forcing on North American monsoon moisture surges. *J. Clim.* 31, 7949–7968.

Ratner, B. (2009). The correlation coefficient: its values range between+ 1/- 1, or do they?. *J. Target. Meas. Anal. Market.* 17, 139–142. doi: 10.1057/jt.2009.5

Ropelewski, C. F., and Halpert, M. S. (1986). North American precipitation and temperature patterns associated with the El Niño/ Southern Oscillation (ENSO). *Mon. Weather Rev.* 114, 2352–2362. doi: 10.1175/1520-0493(1986)114<2352:napatp>2.0.co;2

Scanlon, B. R., Keese, K. E., Flint, A. L., Flint, L. E., Gaye, C. B., Edmunds, M., et al. (2006). Global synthesis of groundwater recharge in semiarid and arid regions. *Hydrol. Process.* 20, 3335–3370. doi: 10.1002/hyp.6335

Schussman, H., and Gori, D. F. (2004). *An ecological assessment of the Bureau of Land Management's Current Fire Management Plans: Materials and Recommendations for future fire planning*. Arizona: The Nature Conservancy.

Sheppard, P. R., Comrie, A. C., Packin, G. D., Angersbach, K., and Hughes, M. K. (2002). The climate of the US Southwest. *Clim. Res.* 21, 219–238.

Shinker, J. J. (2010). Visualizing spatial heterogeneity of western U.S. climate variability. *Earth Interact.* 14, 1–15.

Shinker, J. J., and Bartlein, P. J. (2009). Visualizing the large-scale patterns of ENSO-related climate anomalies in North America. *Earth Interact.* 13, 1–50. doi: 10.1175/2008ei244.1

Stahle, D. W., Cleaveland, M. K., Grissino-Mayer, H. D., Griffin, R. D., Fye, F. K., Therrell, M. D., et al. (2009). Cool-and warm-season precipitation reconstructions over western New Mexico. *J. Clim.* 22, 3729–3750. doi: 10.1175/2008jcli2752.1

Tagestad, J., Brooks, M., Cullinan, V., Downs, J., and McKinley, R. (2016). Precipitation regime classification for the Mojave Desert: implications for fire occurrence. *J. Arid Environ.* 124, 388–397. doi: 10.1016/j.jaridenv.2015.09.002

Turner, R. M., Webb, R. H., Bowers, J. E., and Hastings, J. R. (2003). *The Changing Mile Revisited: An Ecological Study of Vegetation Change With Time in the Lower Mile of an Arid and Semiarid Region*. Tucson: University of Arizona Press, 300.

van der Wiel, K., Kapnick, S. B., Vecchi, G. A., Cooke, W. F., Delworth, T. L., Jia, L., et al. (2016). The resolution dependence of contiguous US precipitation extremes in response to CO2 forcing. *J. Clim.* 29, 7991–8012. doi: 10.1175/jcli-d-16-0307.1

Van Devender, T. R. (1990). Late quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. *Packrat Middens* 40, 134–165. doi: 10.2307/j.ctv21wj578.10

Van Devender, T. R. (1995). "Desert grassland history," in *The Desert Grassland*, eds T. R. Van Devender and M. P. McClaran (Tucson: The University of Arizona Press), 68–99.

Wallace, J. M., and Gutzler, D. S. (1981). Teleconnections in the Geopotential Height Field during the Northern Hemisphere Winter. *Mon. Weather Rev.* 109, 784–812. doi: 10.1175/1520-0493(1981)109<0784:titghf>2.0.co;2

Waters, M. R., and Haynes, C. V. (2001). Late Quaternary arroyo formation and climate change in the American Southwest. *Geology* 29, 399–402. doi: 10.1130/0091-7613(2001)029<0399:lqafac>2.0.co;2

Winkler, D. E., and Brooks, E. (2020). Tracing extremes across Iconic desert landscapes: socio-ecological and cultural responses to climate change, water scarcity, and wildflower superblooms. *Hum. Ecol.* 48, 211–223. doi: 10.1007/s10745-020-00145-5

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