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RESEARCH ARTICLE

# Karuk ecological fire management practices promote elk habitat in northern California

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[Correction added on 28-May-2022, after first online publication: The word 'tribes' has been deleted from the Abstract, point 1.]

## Abstract

1. After a century of fire suppression and accumulating fuel loads in North American forests, prescribed burns are increasingly used to prevent conditions leading to catastrophic megafire. There is widespread evidence that prescribed fire was used by Indigenous communities to manage natural and cultural resources for thousands of years. Wildlife habitat is an example of an ecological response that was actively managed with prescribed burns by Indigenous American peoples and is an important factor in western US forest management planning, restoration and climate resilience efforts.
2. We analysed the effects of modern prescribed burns informed by traditional ecological knowledge (TEK) on the predicted change in elk winter habitat in Karuk aboriginal territory in Northern California between 2013 and 2018 using species distribution and simultaneous autoregressive modelling techniques.
3. Burn types most closely resembling Karuk traditional practices, specifically those incorporating multiple-year broadcast burns, had significant positive effects on elk winter habitat suitability. Conversely, concentrated burns focused solely on reducing fuel loads had significant negative effects on elk winter habitat suitability. However, areas where these fuel-reduction burns were combined with multiple years of broadcast burns featured the highest increases in habitat.
4. *Synthesis and applications*. Our results suggest that transitioning to prescribed burns that more closely follow Karuk traditional ecological knowledge will promote elk habitat in the region. This would be best achieved through continuing to work closely with Indigenous representatives to plan and implement cultural fire prescriptions on a landscape scale, a trend we posit would benefit environmental management efforts across the globe.

KEYWORDS
conservation, ecology, elk, forest management, habitat, prescribed fire, TEK, wildlife

## 1 | INTRODUCTION

Forest landscapes face a variety of threats including climate change, disease, the spread of invasive species and altered fire regimes (Enright et al., 2015; Lesk et al., 2017). Megafires with severe ecological and socioeconomic consequences have become increasingly common, particularly in forests in the Western United States (Jones et al., 2016; Williams, 2013). Forest management practices following Euro-American settlement promoting plantations of reduced tree diversity, a lack of thinning and fire suppression have led to increased tree density and drastically increased fuel loads in many forest ecosystems (Irwin et al., 2018; Ryan et al., 2013). Management efforts in these ecosystems in recent decades attempt to curtail fuel loads through treatments such as selective logging, mechanical thinning and prescribed burning of forests (Hessburg et al., 2016). Effects of climate change such as increased temperatures and drought conditions have resulted in increased megafires globally (Adams, 2013; Meyn et al., 2010), but a recent analysis of wildfire history in California found that land ownership, firefighting policy and land protection status have had stronger effects on the increasing frequency and severity of fires in the last 65 years (Starrs et al., 2018). This suggests that forest management actions such as prescribed burning and mechanical thinning have great potential to reduce megafires in the face of accelerating climatic changes in the Anthropocene (Adams, 2013; Williams, 2013). In the mixed-coniferous forests of the coastal ranges of Northern California, there is an evidence for a particularly drastic increase in fire-return interval (up to a 10-fold increase) and associated accumulations of fuel since Euro-American colonization that (Taylor & Skinner, 2003) although there is also evidence from nearby forests across the Oregon border that historical fire regimes were highly variable with some multi-decade periods without fire (Colombaroli & Gavin, 2010).

Indigenous American peoples used intentional burns to manage multiple ecosystem services and conditions for specific food, fibre, medicinal and cultural resources for thousands of years (Gassaway, 2005; Keeley, 2002). This management practice was typically characterized by increased fire frequency and lower severity compared to those expected by climatic conditions and shaped many North American ecosystems over thousands of years (Ryan et al., 2013; Taylor et al., 2016). Intentional burns by Indigenous communities likely also reduced the spread of larger wildfires (Taylor et al., 2016). Changes to this managed fire regime began after European colonization and subsequent massive reductions to Indigenous populations resulting from novel diseases, warfare and forced removals (Lindsay, 2012; Taylor et al., 2016). Moreover, traditional Indigenous landscape management practices, including prescribed burning, were frequently made illegal during the rapid Euro-American settlement of the continent (Norgaard, 2014), most formally in the Forest Service policies initiated in the early 1900s. The recent emergence of prescribed fire in forest landscape management in North America is thus less a novel development than a return of anthropogenic influences from pre-Euro-American settlement, though how modern practices developed and their degree of resemblance to those of indigenous peoples varies widely (Miller, 2020). It would follow that informing modern management with traditional ecological knowledge (TEK) developed over hundreds or thousands of years in relevant landscapes should help to achieve desired socio-ecological outcomes (Berkes et al., 2000), and Indigenous use of fire is an excellent example of this (Hoffman et al., 2021). In Northern California coast ranges, there is strong evidence that traditional fire practices maintained more open, shade-intolerant plant communities conducive to subsistence and cultural needs than would otherwise be present given the environmental conditions (Crawford et al., 2015).

Wildlife and their habitat are critical socio-ecological resources that display complex and dynamic responses to fire (Moe et al., 1990; Raynor et al., 2015). Better understanding and promoting indigenous burning practices and their effect on wildlife habitat is a promising avenue for more closely linking forest management and wildlife conservation, topics that would benefit from further integration (Irwin et al., 2018). Ungulate populations are an example of wildlife that are extensively managed based on hunting offtake, population trends and habitat responses across the United States (Bender, 2006; Festa-Bianchet, 2007). Ungulates are also a culturally important resource for many Indigenous communities and long connected with fire management and subsistence hunting practices (Drucker & Philip, 1937; Norgaard, 2014). While ungulate responses to wildfire have been studied extensively (Cherry et al., 2017; Raynor et al., 2015), there has been relatively less research on the effects of prescribed burns (Volkmann et al., 2020). Like other taxa, varied ungulate responses to both wild and prescribed fire have been found in forest ecosystems (Biggs et al., 2010; Eckrich et al., 2019; Horncastle et al., 2013; Long et al., 2008). Additionally, the majority of work has analysed individual animal responses without scaling to the population level, and there is a paucity of research about either wildfire or prescribed burn effects on ungulate habitat suitability (Volkmann et al., 2020). Finally, there has been minimal research into the effects of burn practices more closely resembling Indigenous traditional practice in comparison to modern prescribed burn implementations as they relate to wildlife. To help fill these knowledge gaps and more closely link forest and wildlife management, we investigated the effects of prescribed burns on the change in elk habitat suitability in their winter range throughout the Karuk Aboriginal territory in Northern California using species distribution modelling (SDM) and spatial autoregressive (SAR) modelling methods. We hypothesized that all prescribed burns would have a positive effect on elk habitat. Additionally, we hypothesized that areas burned following Karuk TEK, particularly cyclical multiyear broadcast burns, would have the largest positive effect.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Our study area consisted of the 1.4-million-acre Karuk Aboriginal Territory, with more focused sampling around the Western Klamath Restoration Partnership (WKRP) Somes Bar Study area (Figure 1).

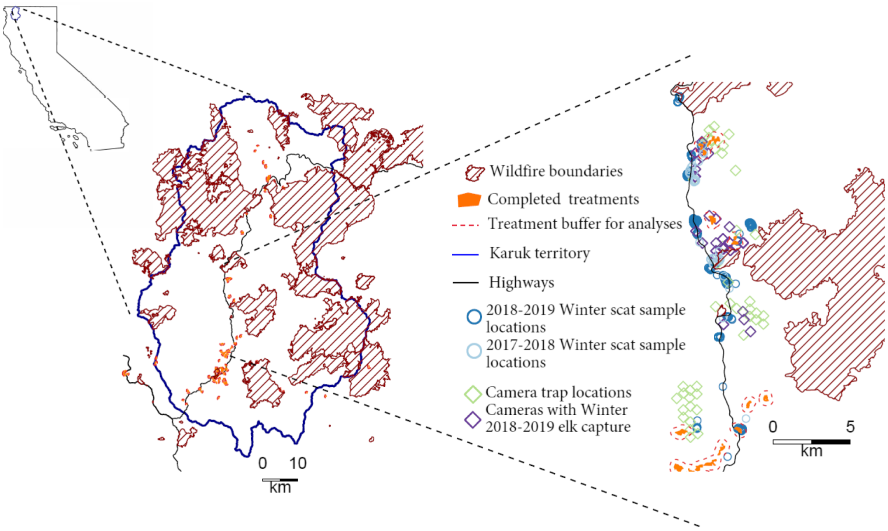


**FIGURE 1** Map of the study system, with Karuk aboriginal territory inset on a map of California. The second inset depicts the focal area for elk data collection, with points representing elk scat locations or camera trap locations, and hatched polygons representing wildfire perimeters for fires that occurred during the study period (2013–2018). Orange filled polygons represent completed prescribed burns during the study period and the red dotted lines represent the 300 m buffer around treatments used to define study areas for prescribed burn effects

The Karuk Tribe and their lands represent a continuously settled culture from time immemorial, and despite extensive persecution after Euro-American colonization they were not forcibly displaced from their ancestral territory (Salter 2003). This territory is part of the floristically diverse Klamath ecoregion dominated by mixed broadleaf/coniferous evergreens and a Mediterranean climate (Sawyer, 2006). Elk is a culturally important species that traditionally made up an important food source (Norgaard, 2014). Karuk tribal members have long managed elk habitat and hunted elk for food, materials, medicine and regalia in their aboriginal territory in northern California (Drucker & Philip, 1937; KDNR 2011). Karuk traditional laws, oral traditions and ceremonies incorporate specific land management practices for elk, including seasonal application of prescribed fire to support elk habitat and regulation of take for subsistence, ceremonial and commercial use based on seasonal ecological indicators and herd population dynamics (KDNR, 2011; Sarna-Wojcicki, 2015). Due to fire suppression, habitat loss and hunting for meat and hides, nearly all elk were extirpated from the Karuk Tribe's aboriginal territory as early as the 1870s (Harper et al., 1967). Beginning in 1985, six Roosevelt Elk *Cervus canadensis roosevelti* from Redwood National Park were re-introduced into Elk Creek in Klamath National Forest. By 1996, 232 Roosevelt elk had been re-introduced into Klamath National Forest and the Marble Mountain wilderness by the US Forest Service and California Department of Fish and Wildlife (Allison et al., 2007). These efforts were successful, and there now exist at least four elk subpopulations in the Marble Mountains with a total population estimate of up to 3,000 animals (Allison et al., 2007).

Elk around the Klamath maintain distinct seasonal ranges, and we focused our study in their winter range due to data availability and the fact that it is their most limited range in terms of habitat (Allison et al., 2007). We focused our research in areas less than 780 m in elevation—we chose this elevation threshold because 95% of elk relocations between November and April fell below 680 m (unpublished data), which we buffered by 100 m to capture the vast majority of elk winter activity.

## 2.2 | Prescribed burns

We analysed a series of prescribed burns conducted within Karuk ancestral territory between 2013 and 2018 to investigate prescribed burning effects on elk winter habitat suitability. These burns were not specifically designed for our study, but elk were one of five focal species whose response to fire a subset of the burns in our study area were designed to consider through the Somes Bar Integrated Fire Management Project (USFS, 2018). A few units and prescriptions in our study were thus designed to enhance Elk habitat features (e.g. meadows/grasslands, forage species, calving habitat, movement/migration corridors), but the vast majority were not designed specifically to benefit elk habitat (USFS, 2018). Karuk cultural practitioners were either directly involved or consulted in the planning and implementation of many of the treatments and completed prescribed burns (USFS, 2018; WKRP, 2014).

Specifically, the prescribed burns consisted of hand-pile, jackpot and broadcast burns. Hand-pile burns involve gathering fuel from the understorey by hand, piling this fuel into small stacks and burning them. Jackpot burns involve burning concentrated areas of fuel but leaving other areas unburned. Both hand-pile and jackpot burn treatments involved some manual thinning of live vegetation by hand, but no use of heavy equipment. Although some traditional Karuk burns resembled hand-pile and jackpot burns, especially to reduce filbert worm and filbert weevil acorn pests (Halpern, 2016; Tripp et al., 2017), the hand-pile and jackpot burns done in our study period were designed in a contemporary context to reduce the large fuel loads resulting from decades of fire suppression policies. Broadcast burns involve a larger, controlled burn of varying portions of the understory or an open area in which the fire is allowed to spread. Though the total areas with hand-pile and jackpot treatment types (4,761 cells or 4.28 $km^2$) was about the same as those with broadcast burns (4,775 cells or 4.30 $km^2$), the actual area burned was higher for broadcast burns due to the spotty, concentrated burning of fuel in the hand-pile/jackpot burn treatment areas. Generally, Karuk traditional fire management consisted of broadcast burns on a repeated basis with temporal intervals that varied based on the specific plant species and desired effects (Tripp et al., 2017).

Because of our multi-year study period, several areas on the landscape featured different prescribed burns in different years. Over the 5 years of the study, this resulted in 17 different categories of burn combinations across the 5 years (e.g. broadcast burn in the first 2 years vs. hand-pile burn in the first year and broadcast burn in the third year). We consolidated these many combinations into six categories by grouping hand-pile and jackpot burns due to their inherent similarity and collapsing pixels that had a given burn type in more than one year into a 'multi-year' category. For example, areas that were burned in two different years with broadcast burns and areas that were burned in three different years with broadcast burns were both categorized as 'multi-year broadcast burns'. Given the fact that traditional Karuk fire management practices generally consisted of cyclical broadcast burns, the 'multi-year' broadcast burn category can be considered the prescribed burn pattern that most closely follows Karuk TEK, whereas the hand-pile and jackpot burn types were more focused on reducing fuel loads in a modern context.

## 2.3 | Elk presence data

We used elk scat locations recorded during non-invasive scat DNA surveys around the Klamath River in the Winter of 2018–2019 as our primary presence records. Scat was collected systematically throughout the elk winter range but represents presence-only data given the difficulty in assessing true elk absences. To supplement these data, we also included elk detected in the same time period on 70 game cameras set up in four focal areas that were spaced 500 m apart on a hexagonal grid pattern within each area (Figure 1). As independent validation data, we used a set of elk presence locations consisting of scat and track records from the area collected in the Winter of 2017–2018. For all elk scat/sign records, we censored duplicate records that fell within the same 30 m cell (the grain size of our environmental data) to avoid oversampling the same environmental conditions. Because our research involved only the non-invasive collection of scat samples and camera trapping, we did not require an ethics evaluation for animal use. Additionally, we did not require permits for field sampling in our study area.

## 2.4 | Environmental data

To estimate habitat suitability, we related elk presence locations to several vegetation variables characterizing the percent cover of shrubs, annual forbs and grasses, perennial forbs and grasses, and trees at a 30 × 30 m resolution and annual timescale acquired from the Rangeland Analysis Platform (RAP) (Jones et al., 2018). These variables were derived through Random Forests modelling of Landsat records, meteorological grids, abiotic land surface maps and field plots across the Western United States (Jones et al., 2018). Although we did not have an appropriate validation dataset for the RAP data in our study area, we used qualitative estimates of grass/forb, shrub and tree cover made at each sampled scat location as a rough check of the RAP variables. This analysis indicated that the general vegetation cover trends observed on the ground were positively correlated with those estimated from the RAP, though this correlation was low and there was wide variability between the two (see Figure S3). A full ground-truthing vegetation survey was beyond the scope of this study, but we posit that the rigorous methodology linking remotely sensed and field plot data to derive cover estimates in the RAP made it the most effective tool available to us to assess spatiotemporal trends in vegetation conditions (Jones et al., 2018). We included only vegetation cover variables as predictors of habitat suitability to explicitly analyse annual elk forage and biophysical habitat structure dynamics that might result from prescribed burns. As control variables for our downstream models of change in habitat suitability, we included terrain ruggedness, elevation and slope aspect (degree direction that the slope faces) to account for other factors that might affect habitat suitability via changes to vegetation growth. We used the USGS National Elevation Dataset (NED) at 30 m resolution for the elevation data, and calculated TRI and slope aspect from this dataset using the 'terrain' function in the 'raster' package in R (Hijmans, 2020; R Core Development Team, 2019). In addition to prescribed fire, our study system has seen large wildfire events in recent decades (1,410.51 $km^2$ across the entire Karuk Aboriginal Territory). Because wildfire has significant effects on vegetation communities and thus elk habitat, we included a binary wildfire/no-wildfire burn control variable capturing any wildfire burns within the study period of 2013–2018. We downloaded area-burned data from the CalFire wildfire perimeter online database (Protection, 2021).

## 2.5 | Habitat suitability modelling

To develop predictions of elk habitat suitability for 2013 and 2018, we trained 'MaxEnt' maximum entropy models on the scat sample locations from the 2018 winter survey effort and several vegetation indices described above in R (Phillips et al., 2017). We used a 'cloglog' link with model predictions ranging from 0 to 1, representing occurrence probability or a habitat suitability index (HSI). We used the 'cloglog' link over a logistic link due to its stronger theoretical justification over the logistic link based on recent derivations of 'MaxEnt' as an inhomogeneous Poisson process (Phillips et al., 2017). 'MaxEnt' models the presence records with this inhomogeneous Poisson-distributed process and relates environmental conditions at the presence locations to typical environmental conditions estimated with random 'background' locations through lasso and elastic-net regularized generalized linear models (Phillips et al., 2017). We randomly chose 10,000 cells from an 800 m buffered area around scat sampling and camera locations to serve as background locations. We chose an 800 m buffer instead of the wider landscape to better approximate background environmental conditions in the area sampled for elk presence. We used the 'ENMevaluate' function in the 'ENMeval' R package to train models across a range of hyperparameters in the 'maxnet' open-source R implementation of MaxEnt (Muscarella et al., 2014; Phillips et al., 2017). Specifically, these included regularization multipliers of 0.5, 1, 1.5 and 2 representing increasing smoothing in model predictions of habitat suitability, as well as all combinations of linear and quadratic feature classes representing increasing model complexity. All models were trained with a random subset of 80% of the presence locations and evaluated with the remaining 20%, repeated five times each. We chose this proportion of training/testing data to maximize the data available for model training while still preserving a sizable dataset for model evaluation, and it has proven an effective ratio in previous evaluations of cross-validation data proportioning (Rajabi et al., 2021). Models were tested for predictive accuracy with the area under the receiver operating curve (AUC) and maximum true skill statistic (TSS), and parsimony with AICc (Allouche et al., 2006; Burnham & Anderson, 2004). Because we aimed to transfer these models to the broader landscape and backwards in time, we chose the most parsimonious (lowest AICc) model to use for predicting habitat suitability. We further validated the accuracy of this model with an independent scat dataset described above using the same AUC and TSS metrics.

### 2.6 | Estimating prescribed burn effects on elk habitat suitability

To estimate the effects of different prescribed burns on elk habitat suitability, we used the per 30 m pixel change in habitat suitability as our response variable. Specifically, our 2013 predictions of habitat suitability used the model trained in 2018 but RAP estimates of vegetation cover in 2013 as the environmental predictors. We then subtracted the 2013 suitability values from the 2018 suitability values to derive a 'change in habitat suitability' raster in which positive values represent improved habitat. We took several steps to account for environmental factors not measured by our SDM. Specifically, we restricted our analysis to areas nearby the prescribed burns by buffering them by 300 m. This also served to reduce the number of our observations (individual pixels describing HSI change) from millions across the landscape to thousands within our buffer. We also included elevation, terrain ruggedness and aspect as control variables that might affect the structural habitat suitability predicted by our model to better isolate prescribed burn effects. To account for the circular nature of the aspect variable, we included its quadratic term in the model. Finally, because adjacent and nearby 30 m pixels are spatially autocorrelated and thus not independent samples, we fit a spatial autoregressive (SAR) model estimating the effects of different prescribed burn types, the age of the most recent burn and our control variables on HSI change using the 'spautolm' function of the 'SPATIALREG' R package (Bivand et al., 2008). SARs estimate a spatial lag parameter which accounts for the dependence of an observation on those in nearby areas through a regression on their residuals (Bivand et al., 2008). We compared our spatial model with a null model assuming no spatial dependence and presented the most supported results, with parameter coefficients of the SAR interpretable as a standard regression model.

## 3 | RESULTS

A total of 748 separate scat samples were collected and georeferenced in the Winter of 2018–2019. In all, 498 of these samples fell into unique 30 m raster cells, and the 250 additional samples that were found in cells that already featured an elk presence location were removed from the analysis. Of the 70 camera traps operating in our winter study period, 26 captured elk presences. The independent elk sign sampling effort in the Winter of 2017–2018 resulted in 38 presence locations, 36 of which fell into unique 30 m raster cells and were kept for model validation (Figure 1).

Our top habitat suitability model included linear and quadratic terms and a regularization factor of 0.5. The model predicted decreasing habitat suitability with increasing tree, shrub, and litter cover, and increasing habitat suitability with increasing annual grasses and forbs cover (Figure 2). The model showed good accuracy in predicting elk presence in both the Winter of 2018–2019 (AUC = 0.88, TSS = 0.66) and the Winter of 2017–2018 (AUC = 0.85, TSS = 0.54). Our model predictions indicated wide spatial variability in elk winter habitat suitability across the landscape, and generally increasing suitability from 2013 to 2018 (Figure 3).

In our study period, single year broadcast burns were the most common burn type (3,499 cells or 3.15 $km^2$), followed by jackpot/hand-pile burns (3,407 cells or 3.10 $km^2$), multiyear broadcast burns (665 cells or 0.60 $km^2$), single year broadcast and single year jackpot/hand-pile burns (655 cells or 0.59 $km^2$), multiyear broadcast and single year jackpot/hand-pile burn (611 cells or 0.55 $km^2$), and multiyear jackpot/hand-pile burns (88 cells or 0.08 $km^2$, Table S1). Our SAR model results indicated that there was significant spatial autocorrelation between HSI pixels and that including a spatial dependence parameter (lambda) improved model fit (Table 1). All prescribed burn types had significant effects on Winter elk habitat (Table 1). Pixels that had a single year of broadcast burns had HSI change values about 5% greater than those with no burns, and this effect was nearly doubled in pixels with multiple years of broadcast burns (9%). Jackpot and hand-pile burns on their own had negative effects on HSI change, but when combined with multiple years of broadcast burning had the largest positive effect on HSI change at 23% higher than unburned areas (Table 1). Increasing age of the most recent burns had a significant positive effect on HSI change increasing 1% per year (up to the possible 5-year-old burns included in this study).

## 4 | DISCUSSION

Our results suggest that prescribed burns have variable but generally positive effects on elk winter habitat suitability on a landscape that featured a general trend of increasing suitability over

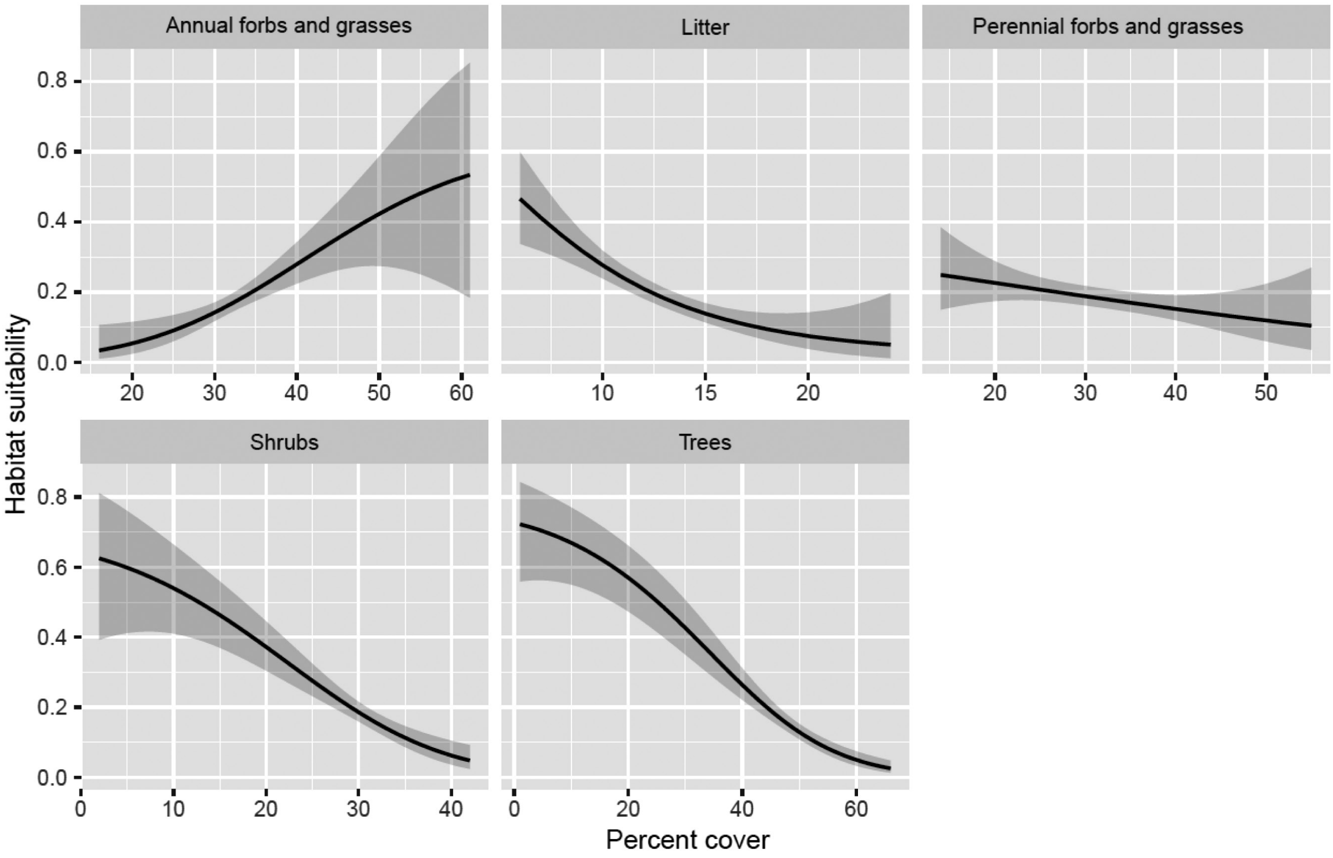


FIGURE 2 Elk winter habitat suitability responses to vegetation cover classes

time. This background trend of increasing winter habitat suitability may reflect changes to vegetation structure based on patterns of historical wildfires, land use transitions and/or climatic patterns in the study system, but we found substantial effects of prescribed burn patterns on top of that background change. Our model results suggest that wildfire resulted in an approximately 4% increase in elk winter HSI, and wildfires before our 2013 study period cut-off likely also played a role in the background trend of increasing HSI that we found. Traditionally, cyclical broadcast burns with variable intervals depending on the species targeted for enhancement were the preferred method of fire management implemented by the Karuk Tribe (Anderson, 2005; Marks-Block et al., 2019). Areas in our study system that resembled this traditional cycle through the implementation of repeated broadcast burns featured much higher increases in modelled elk winter habitat suitability compared to unburned areas, providing strong evidence for the efficacy of management based on Karuk TEK for this goal. While jackpot and hand-pile burns may be necessary in a contemporary context to reduce high fuel loads that have resulted from a century of fire suppression policy, our results suggest their implementation alone has had a negative effect on modelled elk winter habitat. This may be due to the fact that concentrated burns of fuels generally do not clear shrub cover and may in fact allow for increased shrub growth, which have a negative effect on elk winter HSI based on our models. That said, coupling jackpot and hand-pile burns with multiple years of broadcast burns had the largest positive effect on elk habitat change with 23% higher change values than the unburned control pixels. This suggests that coupling burns focused on intensive fuels reduction with multi-year broadcast burn patterns is an effective way to concurrently manage for wildfire risk and elk habitat.

Our findings that broadcast burns improved modelled elk winter habitat suitability are consistent with the fact that these treatments were informed by Karuk TEK and designed to improve wildlife habitat (Drucker & Philip, 1937). The return of prescribed burning to the landscape is part of a cultural and ecological revitalization effort in the Klamath river Basin, a revitalization for which fire is considered by the Karuk to be a central and key component (Lake et al., 2010). Though we focused solely on elk habitat, the Karuk TEK-informed management is targeted at restoring a wide range of habitat for diverse species and enhancing culturally important resources across the socio-ecological landscape (Marks-Block et al., 2019; Tribe, 2019). Though our socio-ecological 'response' in this study—the restoration of elk winter habitat—was narrower than this broader perspective, our results are an indication that returning tribal management practices to the landscape in the Karuk's ancestral territory is having a positive effect on important target species.

Many studies posit that the effects of fire on ungulate forage availability and/or quality are likely the main mechanism involved in selection responses to fire, but generally this mechanism is not analysed or it is done at a small, vegetation plot-level scale (Eckrich et al., 2019; Horncastle et al., 2013; Lashley et al., 2015). Our

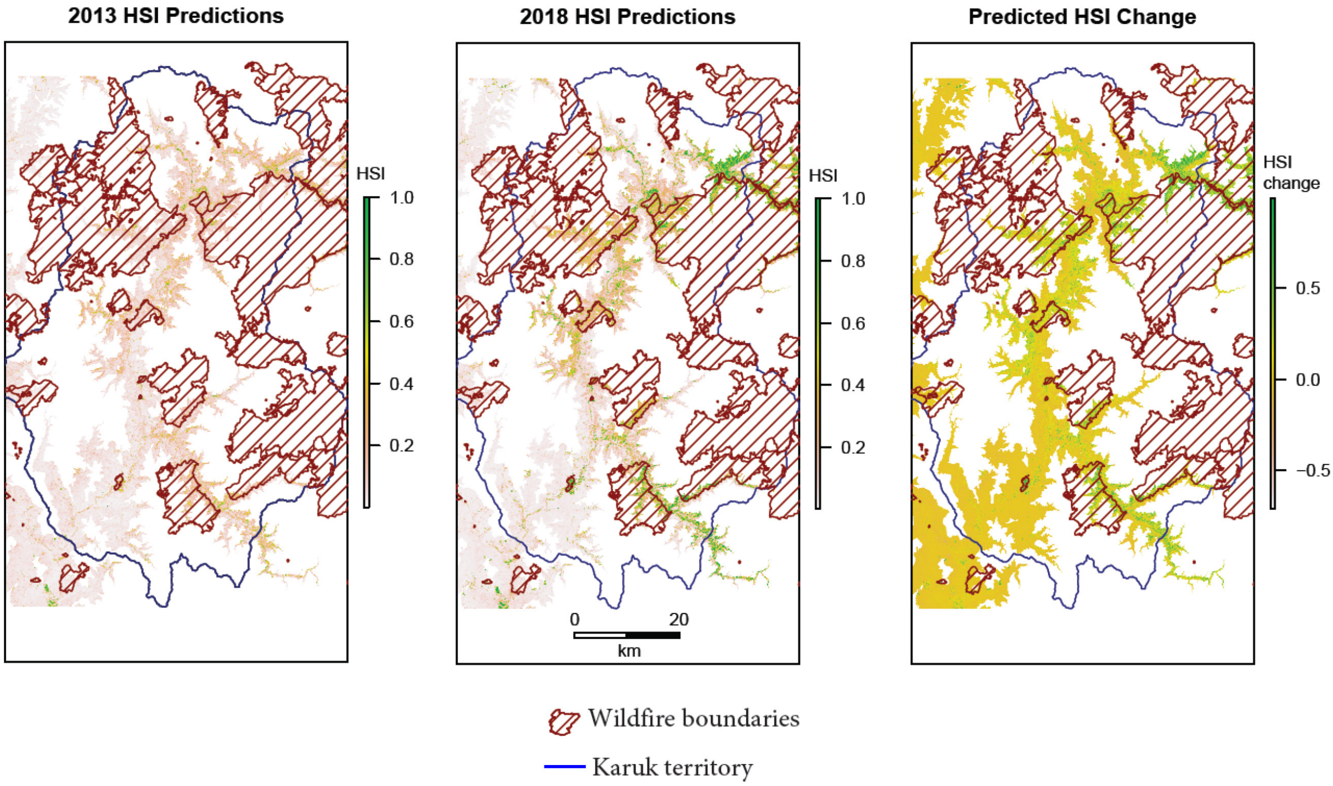


**FIGURE 3** Predicted elk winter habitat suitability across Karuk ancestral territory in 2013 and 2018, and the change in predicted winter habitat suitability between those years. White areas are high elevation regions outside elk winter range, and hatched red polygons represent wildfire boundaries

**TABLE 1** Simultaneous autoregressive model results of prescribed burn effects on 2013–2018 change in HSI. Coefficient estimates of the corresponding variable can be interpreted as the average percent change in a pixel's predicted change habitat suitability based on that variable (a given treatment or a unit change in one of the continuous control variables). Lambda is the autoregressive parameter that accounts for spatial non-independence between observations

| Variable | Coefficient estimate | Coefficient standard error | *t*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | 0.20 | 0.03 | 6.05 | <0.01 |
| Treatment—Broadcast burn | 0.05 | 0.01 | 6.00 | <0.01 |
| Treatment—Jackpot/hand-pile burn | −0.02 | 0.01 | −1.96 | 0.05 |
| Treatment—Multiyear broadcast and jackpot/hand-pile burn | 0.23 | 0.02 | 7.40 | <0.01 |
| Treatment—Multiyear broadcast burn | 0.09 | 0.01 | −2.99 | <0.01 |
| Treatment—Multiyear jackpot/hand-pile burn | −0.11 | 0.04 | 6.05 | <0.01 |
| Age | 0.01 | 2.95E-03 | −5.52 | 0.16 |
| Elevation | −3.13E-04 | 5.68E-05 | 0.67 | <0.01 |
| TRI | 1.17E-03 | 1.75E-03 | 1.77 | <0.01 |
| Aspect | 2.20E-04 | 1.24E-04 | −2.96 | <0.01 |
| Aspect$^2$ | −1.01E-06 | 3.40E-07 | 3.53 | <0.01 |
| Wildfire | 0.04 | 0.01 | 6.05 | |
| Lambda | 0.91 | 0.01 | — | <0.01 |

combination of species distribution modelling using landscape-scale vegetation metrics derived from satellite-based remote sensing and a subsequent model of prescribed burn effects on predicted habitat suitability allows a spatially broader perspective on prescribed burn effects. We posit that compared to the jackpot and hand-pile burns alone with no follow-up treatment, the increased fire coverage associated with broadcast burns cleared more shrubs and woody vegetation, allowing for increased growth and cover of the annual grasses and forbs that our SDM showed elk respond positively to at the landscape level. Increased age of the latest burn also slightly increased the change in habitat suitability, indicating there is a lag-effect in which habitat improves.

Considered together with the positive effect of multi-year burns, this suggests that the most effective prescribed fire management strategy for elk winter habitat in our study area would consist of multiple patches of cyclical broadcast burns on a rotating schedule, potentially after any dense fuel loads are removed through hand-pile and/or jackpot burns. This strategy would fit well into Karuk TEK-informed simultaneous management of multiple culturally important resources on the landscape.

Another proposed mechanism controlling fire effects on ungulate responses is predation risk (Cherry et al., 2017). Reduction of grass height and woody plant density have been hypothesized to reduce predation risk for ungulates in some African savannah settings due to the reduced ambush success rate of predators (Hopcraft et al., 2005; Riginos, 2015; Wilsey, 1996). Conversely, in areas with dominantly cursorial predators like wolves, ungulates may seek increased vegetation cover as refugia (Creel et al., 2005). In our study system, mountain lions, an ambush predator, are the main source of predation risk outside of the hunting and calving season. The direction of fire effects on elk Winter habitat suitability is thus likely the same for both forage availability and predation risk, with more grasses and forbs providing better forage and less cover for ambush. That said, response to predation risk may be different and much larger in other seasons, particularly when young calves are vulnerable to predators of different hunting modes such as black bear (opportunistic) (White et al., 2010). If this is the case, lack of concealment in burned areas may present a trade-off between predation risk and forage quality at certain times of the year (Cherry et al., 2017). The potential expansion of grey wolves into our study system in the near future (Creel et al., 2005; Kovacs et al., 2016; Riginos, 2015) may also affect elk responses to vegetation cover and prescribed burns across all times of the year.

Although the winter range examined is considered the most spatially and resource-limiting seasonal habitat for elk in our study system (Allison et al., 2007), future work should examine both the migration and summer ranges to parse out potential seasonal effects of fire treatments on elk habitat suitability (Long et al., 2008). Our study was also limited in duration due to the increasing uncertainty in the accuracy of elk habitat suitability predictions as we project our SDM further back in time (Werkowska et al., 2017). Due to this, longer term habitat effects may be missed in our relatively short (5 years) time-scale. For example, the transition from grass and forb succession to shrub succession is likely to occur at a longer time-scale dependent on site-specific factors such as canopy cover, species composition and the seedbank composition (Bates et al., 2011). A better understanding of these transition periods and elk use of habitat within them is needed to inform ideal cyclical patterns for repeated burns to promote elk populations. A dedicated ground-truthing vegetation survey across our study area would better validate the use of remotely sensed RAP vegetation cover in our study system, and allow for an analysis of prescribed burn effects on more detailed habitat factors at a finer scale than vegetation cover such as palatable new growth and digestible energy (Rowland et al., 2018).

Further important directions include tracking the overall extent of wildfire (and its severity), climate and prescribed burn types while monitoring elk responses, because these responses may change based on the background landscape, climate and fire regime conditions (Nimmo et al., 2019). Given the large area covered by wildfires in Western North America in the recent past and foreseeable future, wildfire must be considered when designing prescribed burn treatments for positive habitat effects. A larger GPS-collar dataset will aid in this understanding through the direct monitoring of elk use vs. availability of and movement through different types of burned areas as opposed to modelling habitat suitability as an intermediate step to determining prescribed burn effects. That said, we argue that modelling structural habitat suitability through elk presence and remote sensing data was an effective way to estimate broad, landscape-level structural habitat effects of different prescribed burn patterns. A continuing, annual Tribal wildlife research programme would solve the above data and time-scale issues by allowing for more precise monitoring of elk responses to prescribed burns over a longer time span and to wider conditions.

In addition to the implications for elk management in the Klamath River Basin, we argue that this study presents a compelling modelling framework with potential for broader application. Our spatially buffered sampling design and inclusion of control variables allowed us to more closely model treatment effects by minimizing bias, and the SAR model formulation accounted for the inherent spatial autocorrelation in our response variable (HSI change). Our framework also allows for the prediction of future prescribed burn effects on elk Winter habitat suitability across the landscape given the conditions found there, which will help bridge the gap between forest management and wildlife conservation (Irwin et al., 2018). Adopting a spatially explicit approach across wider habitat restoration and monitoring efforts will aid in more accurately evaluating any restoration treatment and better inform conservation action (Tuanmu et al., 2016). Finally, our results provide evidence for the efficacy of incorporating Indigenous knowledge, values and cultural practices into modern wildlife and forest management practices. More collaborative research efforts led by Tribal wildlife and fire scientists and inclusive of Indigenous knowledge and management approaches are urgently needed to revitalize wildlife populations and habitats in the face of rapid environmental change (Hoffman et al., 2021). The benefits of supporting and enhancing Tribal sovereignty and Indigenous knowledge and cultural wildlife management practices in Indigenous lands shown here may inform similar situations across the US West and globally.

## AUTHORS' CONTRIBUTIONS

T.C., B.T., E.T., T.B., D.S.-W., L.M. and J.B. designed the study; T.C., A.H.B., J.C., E.T., B.J.S., W.D. and A.D. collected and analysed data; T.C. wrote the manuscript. All provided feedback in the manuscript writing and revision process and agree on the content.

## CONFLICT OF INTEREST

We have no conflict of interest to report.

## DATA AVAILABILITY STATEMENT

R code and environmental data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.zgmsbccdf (Connor et al., 2022). Elk location data and prescribed burn data will be available by request and approval of the Karuk Tribe Department of Natural Resources.

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## REFERENCES

Adams, M. A. (2013). Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecology and Management*, *294*, 250–261.

Allison, B. L., Creasy, M., Ford, M., Hacking, A., Schaefer, R., West, J., & Youngblood, Q. (2007). *Elk management strategy*. Klamath National Forest.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*, 1223–1232.

Anderson, M. K. (2005). *Tending the wild: Native American knowledge and the management of California's natural resources*. University of California Press.

Bates, J. D., Davies, K. W., & Sharp, R. N. (2011). Shrub-steppe early succession following Juniper cutting and prescribed fire. *Environmental Management*, *47*, 468–481.

Bender, L. C. (2006). Uses of herd composition and age ratios in ungulate management. *Wildlife Society Bulletin*, *34*, 1225–1230.

Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications*, *10*, 1251–1262.

Biggs, J. R., VanLeeuwen, D. M., Holechek, J. L., & Valdez, R. (2010). Multi-scale analyses of habitat use by elk following wildfire. *Northwest Science*, *84*, 20–32.

Bivand, R. S., Pebesma, E. J., & GomezRubio, V. (2008). *Applied spatial data analysis with R*. Springer.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference—Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*, 261–304.

Cherry, M. J., Warren, R. J., & Conner, L. M. (2017). Fire-mediated foraging tradeoffs in white-tailed deer. *Ecosphere*, *8*, 1–11.

Colombaroli, D., & Gavin, D. G. (2010). Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 18909–18914.

Connor, T., Division, W., Tripp, E., Tripp, W., Saxon, B. J., Camarana, J., Donahue, A., Sarna-Wojcicki, D., Macaulay, L., Bean, W. T., Hanbury-Brown, A., & Brashares, J. (2022). Data from Karuk ecological fire management practices promote elk habitat in northern California. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.zgmsbccdf

Crawford, J. N., Mensing, S. A., Lake, F. K., & Zimmerman, S. R. (2015). Late Holocene fire and vegetation reconstruction from the western Klamath Mountains, California, USA: A multi-disciplinary approach for examining potential human land-use impacts. *Holocene*, *25*, 1341–1357.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, *86*, 3387–3397.

Drucker & Philip. (1937). *The Tolowa and their southwest Oregon kin*. Drucker & Philip.

Eckrich, C. A., Coe, P. K., Nielson, R. M., Clark, D. A., & Johnson, B. K. (2019). Effects of underburning on habitat use of mule deer during migration. *Wildlife Society Bulletin*, *43*, 62–70.

Enright, N. J., Fontaine, J. B., Bowman, D., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, *13*, 265–272.

Festa-Bianchet, M. (2007). Ecology, evolution, economics, and ungulate management. In D. G. H. Timothy & E. Fulbright (Eds.), *Wildlife science: Linking ecological theory and management applications* (pp. 183–201). CRC Press.

Gassaway, L. (2005). Native American fire patterns in yosemite valley: A cross-disciplinary study. *23rd Tall Timbers Fire Ecology Conference*, pp. 29–39, Bartlesville, OK.

Halpern, A. (2016). Prescribed fire and tanoak (*Notholithocarpus densiflorus*) associated cultural plant resources of the Karuk and Yurok Peoples of California (PhD). University of California, Berkeley.

Harper, J. A., Harn, J. H., Bentley, W. W., & Yocom, C. F. (1967). The status and ecology of the Roosevelt elk in California. *Wildlife Monographs*, *16*, 3–49.

Hessburg, P. F., Spies, T. A., Perry, D. A., Skinner, C. N., Taylor, A. H., Brown, P. M., Stephens, S. L., Larson, A. J., Churchill, D. J., Povak, N. A., Singleton, P. H., McComb, B., Zielinski, W. J., Collins, B. M., Salter, R. B., Keane, J. J., Franklin, J. F., & Riegel, G. (2016). Tamm review: Management of mixed-severity fire regime forests in Oregon, Washington, and northern California. *Forest Ecology and Management*, *366*, 221–250.

Hijmans, R. (2020). 'raster' R package.

Hoffman, K. M., Davis, E. L., Wickham, S. B., Schang, K., Johnson, A., Larking, T., Lauriault, P. N., Le, N. Q., Swerdfager, E., & Trant, A. J. (2021). Conservation of Earth's biodiversity is embedded in indigenous fire stewardship. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, 1–6.

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*, 559–566.

Horncastle, V. J., Yarborough, R. F., Dickson, B. G., & Rosenstock, S. S. (2013). Summer habitat use by adult female mule deer in a restoration-treated ponderosa pine Forest. *Wildlife Society Bulletin*, *37*, 707–713.

Irwin, L. L., Riggs, R. A., & Verschuyl, J. P. (2018). Reconciling wildlife conservation to forest restoration in moist mixed-conifer forests of the inland northwest: A synthesis. *Forest Ecology and Management*, *424*, 288–311.

Jones, G. M., Gutierrez, R. J., Tempel, D. J., Whitmore, S. A., Berigan, W. J., & Peery, M. Z. (2016). Megafires: An emerging threat to old-forest species. *Frontiers in Ecology and the Environment*, *14*, 300–306.

Jones, M. O., Allred, B. W., Naugle, D. E., Maestas, J. D., Donnelly, P., Metz, L. J., Karl, J., Smith, R., Bestelmeyer, B., Boyd, C., Kerby, J. D., & McIver, J. D. (2018). Innovation in rangeland monitoring: Annual, 30 m, plant functional type percent cover maps for US rangelands, 1984–2017. *Ecosphere*, *9*, 1–19.

Karuk Department of Natural Resources. (2011). *Eco-cultural resource management plan*. pp. 69–70.

Keeley, J. E. (2002). Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography*, *29*, 303–320.

Kovacs, K. E., Converse, K. E., Stopher, M. C., Hobbs, J. H., Sommer, M. L., Figura, P. J., Applebee, D. A., Clifford, D. L., & Michaels, D. J. (2016). *Conservation plan for gray wolves in California*. California Department of Fish and Wildlife.

Lake, F., Tripp, W., & Reed, R. (2010). The Karuk Tribe, planetary stewardship, and world renewal on the middle Klamath River, California. *Bulletin of the Ecological Society of America*, *91*, 147–149.

Lashley, M. A., Chitwood, M. C., Kays, R., Harper, C. A., DePerno, C. S., & Moorman, C. E. (2015). Prescribed fire affects female white-tailed deer habitat use during summer lactation. *Forest Ecology and Management*, *348*, 220–225.

Lesk, C., Coffel, E., D'Amato, A. W., Dodds, K., & Horton, R. (2017). Threats to north American forests from southern pine beetle with warming winters. *Nature Climate Change*, *7*, 713–717.

Lindsay, B.C. (2012). *Murder state: California's native American genocide, 1846–1873*. University of Nebraska Press.

Long, R. A., Rachlow, J. L., Kie, J. G., & Vavra, M. (2008). Fuels reduction in a western coniferous forest: Effects on quantity and quality of forage for elk. *Rangeland Ecology & Management*, *61*, 302–313.

Marks-Block, T., Lake, F. K., & Curran, L. M. (2019). Effects of understory fire management treatments on California hazelnut, an ecocultural resource of the Karuk and Yurok Indians in the Pacific northwest. *Forest Ecology and Management*, *450*, 117517.

Meyn, A., Schmidtlein, S., Taylor, S. W., Girardin, M. P., Thonicke, K., & Cramer, W. (2010). Spatial variation of trends in wildfire and summer drought in British Columbia, Canada, 1920–2000. *International Journal of Wildland Fire*, *19*, 272–283.

Miller, R. (2020). Prescribed burns in California: A historical case study of the integration of scientific research and policy. *Fire-Switzerland*, *3*, 1–19.

Moe, S. R., Wegge, P., & Kapela, E. B. (1990). The INFLUENCE of man-made fires on large wild herbivores in Lake BURUNGI area in northern Tanzania. *African Journal of Ecology*, *28*, 35–43.

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. *Methods in Ecology and Evolution*, *5*, 1198–1205.

Nimmo, D. G., Avitabile, S., Banks, S. C., Bird, R. B., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., … Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, *94*, 981–998.

Norgaard, K. (2014). The politics of **fire** and the social impacts of fire exclusion on the Klamath. *Humboldt Journal of Social Relations*, *36*, 77–101.

Phillips, S. J., Anderson, R. P., Dudik, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*, 887–893.

Protection, S.o.C.a.t.D.o.F.a.F. (2021). *Fire Perimeters through 2020*.

R Core Development Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rajabi, A., Shabanlou, S., Yosefvand, F., & Kiani, A. (2021). *Exploring the sample size and replications scenarios effect on spatial prediction of flood, using MARS and MaxEnt methods case study: Saliantape catchment, Golestan, Iran*. Natural Hazards.

Raynor, E. J., Joern, A., & Briggs, J. M. (2015). Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology*, *96*, 1586–1597.

Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, *84*, 124–133.

Rowland, M. M., Wisdom, M. J., Nielson, R. M., Cook, J. G., Cook, R. C., Johnson, B. K., Coe, P. K., Hafer, J. M., Naylor, B. J., Vales, D. J., Anthony, R. G., Cole, E. K., Danilson, C. D., Davis, R. W., Geyer, F., Harris, S., Irwin, L. L., McCoy, R., Pope, M. D., … Vavra, M. (2018). Modeling elk nutrition and habitat use in Western Oregon and Washington. *Wildlife Monographs*, *199*, 1–6.

Ryan, K. C., Knapp, E. E., & Varner, J. M. (2013). Prescribed fire in north American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment*, *11*, E15–E24.

Sarna-Wojcicki, D. (2015). *Scales of sovereignty: The search for watershed democracy in the Klamath Basin* (PhD). University of California, Berkeley.

Sawyer, J. O. (2006). *Northwest California: A natural history*. University of California Press.

Starrs, C. F., Butsic, V., Stephens, C., & Stewart, W. (2018). The impact of land ownership, firefighting, and reserve status on fire probability in California. *Environmental Research Letters*, *13*, 1–11.

Taylor, A. H., & Skinner, C. N. (2003). Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, *13*, 704–719.

Taylor, A. H., Trouet, V., Skinner, C. N., & Stephens, S. (2016). Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 13684–13689.

Tribe, K. (2019). *Karuk climate adaptation plan*. Karuk Tribe.

Tripp, B., Watts-Tobin, A., & Dyer, J. (2017). *Cultural resources specialist report*.

Tuanmu, M. N., Vina, A., Yang, W., Chen, X. D., Shortridge, A. M., & Liu, J. G. (2016). Effects of payments for ecosystem services on wildlife habitat recovery. *Conservation Biology*, *30*, 827–835.

USFS. (2018). *Somes bar integrated fire management project: Environmental assessment* (U.S.D.o. Agriculture, Ed.). US Forest Service, Siskiyou County.

Volkmann, L. A., Hutchen, J., & Hodges, K. E. (2020). Trends in carnivore and ungulate fire ecology research in north American conifer forests. *Forest Ecology and Management*, *458*, 117691.

Werkowska, W., Marquez, A. L., Real, R., & Acevedo, P. (2017). A practical overview of transferability in species distribution modeling. *Environmental Reviews*, *25*, 127–133.

White, C. G., Zager, P., & Gratson, M. W. (2010). Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management*, *74*, 355–369.

Williams, J. (2013). Exploring the onset of high-impact mega-fires through a forest land management prism. *Forest Ecology and Management*, *294*, 4–10.

Wilsey, B. J. (1996). Variation in use of green flushes following burns among African ungulate species: The importance of body size. *African Journal of Ecology*, *34*, 32–38.

WKRP. (2014). Western Klamath restoration partnership. In W. Harling & B. Tripp (Eds.), *A plan for restoring fire adapted landscapes* (pp. 1–57). US Forest Service.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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