Intermediate fire severity diversity promotes richness of forest carnivores in California

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Abstract
Aim: Fire can strongly influence ecosystem function, and human activities are disrupting fire activity at the global scale. Ecological theory and a growing body of literature suggest that a mixed severity fire regime promotes biodiversity in western North America. Some researchers advocate the use of pyrodiversity (i.e. heterogeneity in aspects of the fire regime such as time since fire or severity) as a conservation index to be maximized. Others caution against this approach arguing that the index over-simplifies fire–biodiversity interactions across trophic, spatial and temporal scales. We evaluated the effects of several landscape-scale pyrodiversity indices, and their severity and time-since-fire components, on species richness of forest carnivores.

Location: Northern California, United States.

Methods: We gathered data on fire history and mammal occurrence from camera trap surveys at 1,451 sites across Northern California public and private forestlands during 2009–2018. We used these data to model the effects of fire severity diversity, and its components (i.e. low, moderate and high severity wildfires), on carnivore richness at short (10 years) and longer (25 years) timeframes. We repeated the modelling using a measure of time-since-fire diversity and its components (<10 years, 10–20 years, 20–30 years, 30–40 years, 40–100 years). We used Bayesian multispecies occupancy modelling to correct for imperfect measurement of species richness.

Results: We found that carnivore richness was highest at locations with intermediate fire severity diversity (0.46, 90%CI: 0.40–0.52) calculated using Simpson’s Measure of Evenness (range: 0–1) for the 10-year timeframe, and the results were almost identical yet less precise for the longer timeframe. When we separated fire severity diversity into its components, we found that carnivore richness was highest at locations where 17% (90%CI: 4–20) of the landscape had experienced low severity burns over the past decade. In contrast, we found no association between time-since-fire diversity and carnivore richness, however, an intermediate amount of one of the components (e.g., the total amount of fire in the past 10 years) was positively associated with carnivore richness. Our results are consistent with a mixed severity fire regime wherein there is a greater extent of low severity than high severity fire.
Main conclusions: Overall our results suggest that carnivores would benefit from landscapes managed for greater, but not maximal, fire severity diversity. Our results also suggest that prescribed, low severity burns may provide ecological services to wildlife not otherwise provided by silviculture in a managed forest landscape.

KEYWORDS
camera traps, hierarchical modelling, mixed severity fire regime, occupancy, optimization, wildfire

1 | INTRODUCTION

Fire can strongly influence ecosystem function and patterns of vegetation and wildlife diversity (Bowman et al., 2009). Climate change and other anthropogenic factors are disrupting fire activity at the global scale which threatens both ecosystems and human health (Kelly et al., 2020; Moritz et al., 2012). Yet, the effects of fire, and changing fire regimes, on wildlife are expected to vary regionally depending on the ecosystem context (Carbone et al., 2019; Geary et al., 2020).

In western North America, wildfire is a key natural disturbance that has shaped the structure and heterogeneity of temperature forests over millennia (Agee, 1998; Mohr et al., 2000; Taylor & Skinner, 2003). Fire and other disturbances leave snags and large woody debris, open up growing space for non-tree vegetation and reset the successional trajectory for new or modified forest stands via a mix of tree regeneration and retention of post-disturbance legacy trees (Franklin et al., 2002). Until the 20th century, frequent fire characterized lower and middle elevation pine and mixed conifer forests that covered large, mountainous portions of the region (Safford & Stevens, 2017). A mixed severity fire regime characterized many of these forests wherein there was a greater extent of low severity fires that thinned out smaller diameter understory trees than high severity fires that destroyed the majority of overstorey trees (Agee, 1998; Steel et al., 2015). Such a regime created mosaics of early and late successional forest structure and composition that supported diverse breeding and foraging needs of numerous wildlife species including spotted owl (Strix occidentalis), black-backed woodpecker (Picoides arcticus), Pacific fisher (Pekania pennanti) and mule deer (Odocoileus hemionus) (Eckrich et al., 2019; Hanson, 2013; Lesmeister et al., 2019; Steel et al., 2015).

Over the past century, however, factors such as climate change, fire suppression and timber harvesting have increased the relative extent of high versus low severity fires in western North American forests (Millar et al., 2007). Consequently, the mean fire return intervals of historically frequent-fire-adapted forests have increased from 10–20 years to (Van de Water & Safford, 2011) to 70–90 years (Safford & Van de Water, 2014). The associated changes in forest structure, characterized by denser stands with fewer older (>250 years) and larger diameter (>60 cm) trees (Beaty & Taylor, 2007; Youngblood et al., 2004), make them more vulnerable to stand-replacing fires (McIntyre et al., 2015). Modern wildfires are also more often larger in size than was the case historically, such that natural forest regeneration is reduced at greater distances from edges increasing the likelihood that these areas are replaced by shrublands and grasslands (Stevens-Rumann & Morgan, 2019). In summary, the altered fire regime has effected changes in forest seral stage distribution and the diverse communities of birds, forest carnivores and other mammals the forests support (Fisher & Wilkinson, 2005; Tingley et al., 2016; Vanbianchi et al., 2017).

Thirty years ago, ecologists introduced the concept of pyrodiversity and posited that managing landscapes for a mosaic of fire return intervals, sizes and severities would increase biodiversity (Martín & Sapis, 1992). Practitioners of this approach have compared species richness to diversity indices (e.g. Shannon or Simpson) of various fire measurements (Farnsworth et al., 2014; Ponisio et al., 2016). Other ecologists, however, cautioned against embracing the “pyrodiversity begets biodiversity” theory in conservation biology, arguing that complex interactions across trophic, spatial and temporal scales need to be better understood and integrated into management (Bowman et al., 2016; Farnsworth et al., 2014). Researchers sometimes conflate a mixed severity fire regime with “pyrodiversity,” in part because definition of the latter has tended to vary by study. Some studies have defined pyrodiversity in terms of fire severity (Ponisio et al., 2016; Steel et al., 2019; Tingley et al., 2016), while others have used time-since-fire measurements (Bliege Bird et al., 2018; Farnsworth et al., 2014) or seral stage diversity as a proxy for post-fire forest conditions (Kelly et al., 2014; Taylor et al., 2012).

Additionally, evaluating a linear relationship between species richness and pyrodiversity defined as a diversity index of the relative areas of fire history or severity classes has provided mixed results (Farnsworth et al., 2014; Ponisio et al., 2016; Taylor et al., 2012). One potential reason for the inconsistencies is that a mixed severity fire regime, in which there is a greater extent of low intensity than high intensity fire, corresponds with intermediate, not maximal, fire severity diversity. He et al. (2019) drew a similar conclusion in relation to pyrodiversity defined in terms of post-fire seral stages, and noted that intermediate pyrodiversity is consistent with the intermediate disturbance hypothesis, which describes a landscape containing a mix of early and late seral habitat conditions as supporting the largest number of species.
The value of pyrodiversity as a conservation metric depends on the clarity of conservation objectives. In restoration ecology, conservation planners use an understanding of the historical natural range of variability of an ecosystem to guide current management goals (Landres et al., 1999; Wiens et al., 2012). In many systems, however, the magnitude of cumulative anthropogenic impacts renders achieving restoration objectives difficult (Jackson & Hobbs, 2009). Restoration of pre-European settlement fire regimes in western North America is unlikely and impractical due to a myriad of socioeconomic, human health and fire safety concerns (Franklin et al., 2014; Millar et al., 2007). Alternatively, reconciliation ecology attempts to increase or sustain current biodiversity within human-dominated landscapes (Hobbs et al., 2009; Rosenzweig, 2003). One approach is to use data on spatial variation in current biodiversity to identify the optimal fire history or mix of severity classes that maximize species richness (Kelly et al., 2014).

Relatively, few empirical studies of fire effects have examined carnivores (i.e. Carnivora), and those that have done so have generally focused on single species, short timeframes and small spatial extents (Volkmann et al., 2020). In California, recent studies have addressed the effects of pyrodiversity on birds (Tingley et al., 2016), bats (Steel et al., 2019), and plants and their insect pollinators (Ponisio et al., 2016). Most carnivore-related fire studies in forested portions of the state have focused on fisher (Pekania pennanti) (Switzer et al., 2016; Truex & Zielinski, 2013; Zielinski et al., 2013). Several studies have examined the effects of fire on carnivores in Southern California, but these investigations either focused on chaparral habitats or high severity fire in conifer forests (Borchert, 2012; Jennings et al., 2016; Schuette et al., 2014). A need remains for more community-level research on the long-term effects of a mixed severity fire regime on forest carnivores as a group and the ecological linkages to their prey (Volkmann et al., 2020). The few studies directly evaluating the community-level effects of pyrodiversity on carnivores or other predators are not from western North America (Bliege Bird et al., 2018; Jorge et al., 2020). The information gap for carnivores is noteworthy to conservation because of their top-down ecological role as predators, lethal control in response to livestock conflicts or property damage, and potential harvest as furbearers (Bergstrom, 2017; Miller et al., 2001).

Our objective was to investigate the effects of landscape-level pyrodiversity on carnivore diversity in Northern California forests in the USA. For a suite of forest-dwelling carnivores, we hypothesized that intermediate amounts of either fire diversity or time-since-fire diversity would maximize site-level species richness (i.e. alpha diversity). Further, we expected that species richness would be greatest where the extent of low severity fires was greater than for high severities fires, because of an expectation that carnivores and their prey are adapted to a mixed severity fire regime that was historically widespread in our study area prior to the 20th century. Lastly, we considered implications for global and regional biodiversity conservation and forest management and needs for additional research.

FIGURE 1 Locations of 1,451 camera trap survey sites in Northern California forests during 2009–2018. Most locations were surveyed during a single year

2 | METHODS

2.1 | Study area

Since 2009, as part of a commitment to long-term monitoring of wildlife populations, the California Department of Fish and Wildlife (CDFW) has used camera traps to systematically survey mammals across a 66,558-km² forested area of Northern California in the USA (Figure 1; Furnas et al., 2017; Gonzales & Hoshi, 2015). The study area includes all, or portions, of the North Coast, Klamath Mountains, Southern Cascades and Northern Sierra Nevada ecoregions (Schoenherr, 1992). Elevations range from 70 m to 4,332 m (mean = 1,340 m, SD = 500 m). Over 70% of the study area was forested with Douglas-fir (Pseudotsuga menziesii) dominated-forests in the west, replaced by Ponderosa Pine (Pinus ponderosa) and White Fir (Abies concolor) to the east. Most of these mixed conifer forests were historically characterized by a mixed severity fire regime (Steel et al., 2015). Average precipitation over the past 30 years has been 1,280 mm/year (range = 300–3,800 mm/year by location). Oak (Quercus spp) dominated forests characterized lower elevations generally below 800 m (Schoenherr, 1992). Rugged topography and climate stability over past millennia have created a globally-important refugia of biodiversity and endemism (Olson et al., 2012).

2.2 | Study design

For 2009 through 2018, we conducted wildlife surveys using camera traps. We attempted random selection of sampling grid hexagons each year without replacement (Cochran, 1977, p. 18) from the Forest and Inventory Analysis (FIA) sampling frame (Bechtold & Patterson, 2005). The distance between adjacent hexagon centres within this grid was 5.35 km. Within each sampled hexagon,
we selected two survey sites ~1.6 km apart such that we eventually included a total of 1,451 sites across the study area. These survey sites occurred on public agency and private industrial forestland ownerships. To the extent practicable, we attempted to randomly select sampling hexagons and survey sites within them, but we were frequently constrained by a variety of factors including land ownership, inaccessible terrain and weather. The primary survey site was usually located at a hexagon centroid, but private property, steep terrain and other logistical issues often required relocating survey sites (~30%) to more accessible locations within selected hexagons. Where relocation was not feasible, the selected hexagon was not sampled. We further limited survey sites to areas surrounded by at least 20 ha of forest in excess of 10% canopy cover. We randomized the locations of secondary survey sites, which also needed to meet the 20 ha and 10% canopy cover criterion; crews drove to a location approximately 1,450 m from the first site as determined by a Global Positioning System device, and then walked until reaching a location 1,600 m from the first site or 200 m from the road.

We assessed potential bias in the placement of our survey sites by comparing habitats at our sites with the distribution of habitats throughout the study area. Specifically, we used the California Wildlife Habitats Relationships (CWHR; Mayer & Laudenslayer, 1988) classification system to classify habitats from a land use land cover map based on Landsat imagery (California Department of Forestry & Fire Protection, 2019).

### 2.3 Camera trap surveys

A “stealth-mode” Reconyx PC 90 or PC 900 infra-red sensor, motion-activated, digital camera (www.reconyx.com) was affixed to a tree at each survey site. It was placed approximately 1 m above the ground aimed at a shallow angle (<20°) towards bait placed 3–5 m distant at the base of a tree. Cameras were set to high trigger sensitivity, three pictures per trigger, one-second trigger interval and no delay quiet period. We baited camera traps with approximately 400 g of chicken parts and 160 g of fish or seafood flavoured cat food in a sock nailed approximately 1 m up the bait tree bole, half an apple impaled on a nail below the sock, 500 ml of oatmeal–peanut butter mixture on a plate surrounded by a ring of sliced apple at the base of the tree and a salt lick placed next to the grain. "Gusto" scent lure (www.minntrapprod.com) was applied to the sock and low hanging branches of at least two nearby trees behind the bait tree. Our survey protocol generally matched the recommendations of Zielinski and Kucera (1995) except that we did not return to rebait cameras for the majority (95%) of survey sites. Our annual survey season began in early August and continued through late November or early December. The duration of surveys was 2–5 weeks, and both camera traps within a hexagon were always surveyed concurrently.

We reviewed photographs from camera surveys to identify all mammal detections to species. We created a detection history for each site that indicated whether (“1”) or not (“0”) a species was observed for each 24-hr survey day up to 30 days. Average survey duration was 18.7 days. If the survey duration was <30 days, or if the camera was not functional some of the time, these days were treated as missing data (“x”) in a full 30-day detection history (e.g. 0000011010100xxxxxx for a 14-day survey). We detected 15 carnivore species (Table 1) at the camera trap sites.

### 2.4 Fire data

We used the Monitoring Trends in Burn Severity (MTBS) spatial database of fire severity of all wildfires >500 ha in the USA since 1984. This database uses a Normalized Burn Ratio based on Landsat
satellite imagery to categorize burn severity (Eidenshink et al., 2007). For each camera trap location, we calculated the cumulative amount of unburnt area and the cumulative amounts of low, moderate or high severity fire during the preceding 10 and 25 years within a 10-km radial buffer adopted to represent the landscape-level habitat context corresponding to the home ranges of multiple individuals within each species (Bennett et al., 2006). We reasoned that the habitat requirements to support a small carnivore population within a buffered area would increase the likelihood of an individual occupying the smaller area in vicinity of the camera trap at the centre of the buffer. To measure fire severity diversity, we computed Simpson’s Measure of Evenness (SME) of the four burn category proportions from MTBS (none, low, moderate, high) at both the 10-year and 25-year timeframes (Smith & Wilson, 1996). We chose the 10-year timeframe because it corresponds to short-term fire effects consistent with the historical fire return interval for low severity fire in many frequent fire adapted forests in California (Safford & Van de Water, 2014). We also chose this timeframe because it matches the repeat survey interval used in some long-term forest inventories (Bechtold & Patterson, 2005) and we were concerned that a shorter interval (e.g., 1, 3 or 5 years) would have insufficient variation in burnt areas for data analysis using our sample. For assessing longer term fire severity effects, we would have preferred to have looked at longer timeframes than 25 years but were limited by the temporal extent of the MTBS data. The 10- and 25-year timespans were determined for each site (i.e., preceding the year a camera trap survey was conducted there).

We repeated a similar analytical process for calculating covariates pertaining to time since fire, although the data available allowed us to inspect a longer timeframe than we used for fire severity. We used fire perimeters dating back to 1901 compiled by the California Department of Forestry and Fire Protection (2019). We then calculated the cumulative proportions of each 10-km buffer burned over the 0–10 years, 10–20 years, 20–30 years and 40–100 years preceding our camera trap survey. We chose these increments in part because they were similar to those used in other time-since-fire studies (Di Stefano et al., 2013; Farnsworth et al., 2014). We chose 10-year increments because of consistency with the repeated survey interval of forest inventories as noted above (Bechtold & Patterson, 2005). We did not look at an interval of less than 10 years in part because recent research from California forests shows that pyrodiversity was a better predictor of wildlife diversity a decade after fires compared to 1-year post-fire (Tingley et al., 2016) and because of the relative sparsity of areas that burnt each year in our sample. We focused on more recent time intervals (up to 40 years) consistent with the short (10–20 years) fire return interval that was historically typical of frequent fire adapted forests of western North America (Van de Water & Safford, 2011). One potential limitation of using fire perimeters is that they usually included unburnt patches, but we reasoned that our landscape-scale time-since-fire analysis addressed the cumulative effects of mixed severity wildfire on small populations of carnivores whose large home ranges overlapped multiple habitat types.

### 2.5 Occupancy modelling

Occupancy represents the proportion of an area in which a species occurs, or the probability that it occurs at a point. Occupancy modelling allows simultaneous estimation of detection and occupancy probabilities using temporally replicated surveys occurring over a time period for which occupancy is assumed to remain constant (MacKenzie et al., 2006). We used multi-species occupancy modelling to combine the survey data from numerous carnivore species wherein occupancy and detection coefficients were species-specific random slopes varying normally around a community mean (Iknayan et al., 2014).

We modelled whether a species $i$ occurred at site $j$: $z_{ij} \sim$ Bernoulli ($p_{ij}$); and whether it was detected in survey $k$: $y_{ijk} \sim$ Bernoulli ($z_{ij} \times p_{ijk}$). Covariates on occupancy ($\psi$) and detection probability ($p$) were modelled via logistic regression. Hyperparameters were placed on all covariates. We first fit eight models representing each of the 10-year and 25-year timeframes and the main effects of fire severity diversity and its three components (e.g., low, moderate, high) including a quadratic term (see equation below) to allow estimation of an optimal amount of fire for maximizing site-level species richness (i.e., alpha diversity). We could not include the six components in the same model because of high collinearity both within and across timescales ($r > 0.8$). Because components were estimated in separate models, different fire effects may explain the same variation and do not represent the isolated effects of each component in the context of the others. We fit two additional models representing time-since-fire diversity and all five of its components in the same model ($r < 0.5$). In all ten models, we controlled for elevation based on the findings of other researchers that mammal diversity is often highest at middle elevations in montane systems (Hodge & Arbogast, 2016; Li et al., 2003). We controlled for the occurrence of older, larger diameter trees (“big trees”), which are important for supporting the resting and denning habitat of Fishers (Zielinski et al., 2004) and American Black Bears (Ursus americanus) (Bull et al., 2000). We also included this covariate to partially address seral stage diversity that may not be fully reflected in our fire history variables due to the wide application of silviculture over the past century that has disproportionately harvested larger and older trees (Collins et al., 2017). We used date (i.e., day of year) and 3-day temporal lag to previous detection (1 or 0) covariates appropriate for explaining heterogeneity of detection probabilities from camera trap surveys (Furnas et al., 2017; Sweitzer et al., 2016). Lastly, we included a covariate to represent various minor protocol differences between surveys implemented by two CDFW administrative regions (Sierra Nevada ecoregion versus all other locations).

\[
\text{logit} (\psi_{ij}) = A0 + A1 \times \text{Fire}_i + A2 \times \text{Fire}_i^2 + A3 \times \text{Elevation}_j + A4 \times \text{Elevation}_j^2 + A5 \times \text{Big Trees}_i + A6 \times \text{Big Trees}_i^2
\]

\[
\text{logit} (p_{ijk}) = B0 + B1 \times \text{Date}_j + B2 \times \text{Date}_j^2 + B3 \times \text{Lag}_j + B4 \times \text{CDFW Region}_j
\]
In one model, that represented the components of time-since-fire diversity, the five fire covariates and their quadratic terms were modelled together. We extracted elevation at each site from the National Elevation Dataset (10-m resolution; U.S. Geological Survey, http://ned.usgs.gov). For big trees, we calculated the proportion of each 10-km landscape buffer containing forest stands with an average tree diameter > 60 cm at breast height (1.5 m above ground) using 30-m raster derived from Landsat imagery ground-truthed against on-the-ground measurements (California Department of Forestry & Fire Protection, 2019).

We solved each occupancy model with a Markov chain Monte Carlo (MCMC) algorithm (Link et al., 2002) implemented in nimble (0.9.1; de Valpine et al., 2017) with the auxiliary package nimbleecology (0.3.0; Goldstein et al., 2020) accessed via R statistical software (3.5.2; R Core Team, 2020). Uninformative priors were assumed for all parameters. Five independent chains each of 30,000 samples were run with a burn-in period of 1,000 and a thinning rate of four. The three pyrodiversity models (severity 10-year and 25-year and time-since-fire) were run for 50,000 iterations rather than 30,000 to achieve estimate convergence. Effective mixing of these chains was assessed by means of the Gelman-Rubin convergence statistic (R-hat < 1.1; Gelman et al., 2004). Consistent with recommendations for monitoring projects, we adopted a Type I error rate of 0.1 (and associated 90% credible intervals) for testing null hypotheses (Bart et al., 2004).

Bayesian models readily facilitate calculation of derived parameters and their posterior distributions (Royle & Dorazio, 2008). We used the pyrodiversity indices and their various components to compute proportion of the landscape buffer in each condition that maximized species richness. Rather than assume random sampling of survey sites from across the study area, we applied model-based inference to extrapolate average species occupancies for the study area using the covariate associations from our modelling (Furnas, 2020; Gregoire, 1998). Specifically, we generated a grid of regularly spaced points across the study area equal to our sample size of camera traps. We calculated covariates at each of those grid points, which we used to calculate predicted species occupancies at each location, and averaged those to represent species occupancy estimates at the study area scale. We also used the grid points to compare our model results against current averages and histograms of pyrodiversity and its components across the study area. We include all of the data used in modelling, R code that fully specifies the models, and the posterior distribution of all parameters as an online supplement (see Supporting Information Data S1).

### RESULTS

We confirmed that the locations of our survey sites were slightly biased towards forested habitats (Table 2). American Black Bear, Mountain Lion (Puma concolor) and Bobcat (Lynx rufus) were the most commonly occurring (ψ > 0.4) species, although expected differences in home ranges among species imply that these occupancy ranks do not equate to relative abundances.

The elevation and big tree covariates were effective at modelling spatial variation in species occurrence. In particular, big trees were associated with occurrence of Fisher, American Black Bear and Ringtail (Bassariscus astutus). Date and the temporal lag covariates were effective in explaining detection probability heterogeneity within species. We did not find any community-level differences in detection probability among the two CDFW administrative regions that contributed camera data (see Supporting Information Data S1 for details of the non-fire results). After controlling for these factors in our models, we found that carnivore richness was greatest at locations characterized by intermediate fire severity diversity (10 years: SME = 0.46, 90%CI: 0.40–0.52; 25 years: SME = 0.48, 90%CI: 0.31–0.61) as compared to an average of 0.33 for the study area. Although the results changed little between the 10-year and 25-year timeframes, the former was more precise. Some species (e.g. Gray Fox and Ringtail) had higher fire severity diversity optimums than others (Western Spotted Skunk (Spilogale gracilis)) (Figure 3). In contrast, we did not find any community-level associations with time-since-fire diversity.

When we modelled the components of fire severity diversity separately, we found credible unimodal (90% credible interval of quadratic term is negative and does not overlap zero) associations between carnivore richness and extent of low severity fire during the 10-year timeframe and high severity fire during both the 10-year

### TABLE 2 Distribution of camera traps by habitat type versus overall distribution of habitat throughout the study area. Habitats were defined using California Wildlife Habitat Relationships (CWHR)

| CWHR type | Per cent of survey sites | Per cent of study area |
|-----------|--------------------------|------------------------|
| Sierran Mixed Conifer | 27.1 | 18.6 |
| Douglas Fir (Pseudotsuga menziesii) | 14.0 | 12.7 |
| Klamath Mixed Conifer | 8.5 | 7.4 |
| White Fir (Abies concolor) | 7.2 | 5.5 |
| Red Fir (Abies magnifica) | 6.8 | 4.3 |
| Ponderosa Pine (Pinus ponderosa) | 6.2 | 5.4 |
| Eastside Pine | 5.5 | 3.7 |
| Montane Hardwood-Conifer | 4.9 | 6.3 |
| Montane Chaparral | 4.6 | 6.4 |
| Montane Hardwood | 4.0 | 6.9 |
| Sagebrush | 1.7 | 2.6 |
| Lodgepole Pine (Pinus contorta) | 1.6 | 0.6 |
| Jeffrey Pine (Pinus jeffreyi) | 1.4 | 1.2 |
| Subalpine Conifer | 1.2 | 0.6 |
| Other | 5.3 | 17.8 |
and 25-year timeframes; however, we did not find any community-level associations with moderate severity fire (Figure 4). The effect of low severity fire during the 10-year timeframe was the strongest association based on the precision of credible intervals. We estimated that carnivore richness was greatest where 17% (90%CI: 4–20) of the landscape burned at low severity over the past 10 years, which scales to an average of 1.7% per year. This amount of burning is greater than the current average annual amount of low severity burnt area within the study area (0.2% per year, Figure 5). When we modelled the components of time-since-fire diversity, we found that only the amount of fire within 10 years and its quadratic term were credibly associated with carnivore richness such that we estimated an optimal amount of recent fire of 3.1% per year (90%CI: 2.3–4.1). We remind the reader that part of the reason this total is larger than the 1.7% optimal extent of annual low severity fire is that the fire perimeters included unburnt patches. It is also larger because it includes the additional extent of moderate and high severity burning. A full reporting of model results is provided in Supporting Information Data S1.

4 | DISCUSSION

Our results provide evidence that an intermediate level of fire severity diversity leads to the greatest site-level species richness of carnivores in Northern California forests. The idea that pyrodiversity...
begets biodiversity has been criticized as too simplistic (Bowman et al., 2016; Farnsworth et al., 2014), and the empirical research evaluating this principle has yielded mixed results (Maravalhas & Vasconcelos, 2014; Parr & Andersen, 2006; Taylor et al., 2012). This uncertainty may in part lie with variation in the use of either severity or time-since-fire measures of diversity and attempts to show that maximum pyrodiversity leads to maximum biodiversity. Our use of both linear and quadratic terms for fire covariates in the occupancy modelling facilitated identification of an optimal intermediate level of pyrodiversity using severity measurements. Our approach is similar to those taken by researchers in Australia to identify optimal fire histories for wildlife using data on either time-since-fire or the distribution of post-fire seral stages (Di Stefano et al., 2013; Kelly et al., 2014). One of these studies (Di Stefano et al., 2013) found that the optimal amount of fire for small mammals and birds included more areas that had not burned in >10 years than those that had burned in ≤10 years, which is consistent with an intermediate level of pyrodiversity calculated using SME for time-since-fire measurements.

Although we did not find a pyrodiversity association using time-since-fire measurements, we found that one of its components (total extent burned in <10 years) was predictive of carnivore richness. In congruence with this result, the 10-year timeframe had the strongest associations in our severity models as evidenced by tighter credible intervals (Figures 3 and 4). These combined findings suggest that the strongest positive effects of wildfire on wildlife may be relatively short term. For example, low severity fire may provide a ~10-year pulse of increased growing space available for herbaceous vegetation and shrubs that provide forage to small mammal prey populations (Amacher et al., 2008; Roberts et al., 2015) and omnivores like bears (Kelleyhouse, 1980; Swanson et al., 2010). Low severity fire can also create forest openings, snags and logs while retaining large diameter overstorey trees (Agee, 1998).

We expect the longer-term effects of high severity fire to include forest regeneration leading to seral stage diversity at the landscape scale, which supports the diverse life history requirements of some carnivores and their prey (Agee, 1998; Hanson & Odion, 2016). High severity fire creates large stocks of snags and downed wood-debris that provide important habitat to some species (Brown et al., 2004; Murphy & Lehnhausen, 1998). In support of these expectations, we identified a credible quadratic fire effect for high severity fire at the 25-year timeframe, but we were unable to estimate a precise optimum (90%CI: 4%–100% of landscape). We speculate that the relative weakness of the high severity fire effect was in part due to a history of silviculture and fire suppression over that past century that has supplanted fire as the primary determinant of seral stage diversity (Collins et al., 2017; Safford & Stevens, 2017). An alternative explanation may be that we were limited to looking at a fire severity timeframe of ≤25 years using the MTBS dataset, and thus lacked statistical power to clearly identify a high severity optimum. We note, however, that we found that three carnivore species (e.g. Fisher, American Black Bear, Ringtail) were associated with big trees in our modelling. This finding highlights the importance of older, larger diameter trees and snags for some carnivores including fisher (Zhao et al., 2012; Zielinski et al., 2004), marten (Delheimer et al., 2019) and black bear (Bull et al., 2000). It also consistent with retaining a portion of the landscape in a condition of older, structurally diverse forests (Hanson & Odion, 2016; Kelly et al., 2014).

Our findings are also consistent with a mixed severity fire regime characterized by intermediate fire severity diversity, in which the extent of low severity fire is greater than that of high severity fire. Specifically, for maximizing carnivore richness, we identified an optimal rate of 1.7% low severity fire extent per year compared to an optimal rate of 3.1% total burning per year which also included unburnt patches within fire perimeters. This comparison suggests that the optimal total amount of combined moderate and high
severity burning (<1.4%, 3.1 minus 1.7) is less than for low severity fire (1.7%). A mixed severity fire regime is likely to provide the right balance of cover, prey, and foraging resources for supporting an abundant and diverse community of carnivores. This conclusion is consistent with the "intermediate disturbance hypothesis" including theoretical predictions that a mixed severity fire regime characterized by an intermediate fire return interval maximizes species richness (He et al., 2019). For example, mixed severity fire regimes are characterized by a right-skewed distribution in the sizes of high severity burnt patches (Perry et al., 2011). This landscape condition, characterized by a greater number of small than large patches, may maximize biodiversity by supporting habitat conditions for a greater number of species (e.g. higher beta and gamma diversities) while still maintaining habitat requirements for species requiring large patches (Arroyo-Rodriguez et al., 2020).

FIGURE 5 Histograms of fire extent by severity class for Northern California forests. The probability distribution represents the chance that a 0.1 increment in percentage of a randomly located 10-km radial area within the study area burnt during a single year.

Our analysis did not address optimal fire associations among the small mammal prey species of the forest carnivores we studied. A full understanding of how pyrodiversity affects carnivore diversity needs to address trophic interactions, because we expect overlap in the habitat conditions supporting carnivores and their prey (Sweitzer & Furnas, 2016). During initial exploration of the camera trap data, we attempted to test the effects of pyrodiversity, and its various severity and fire history components, on the occupancies of the 12 rodent and lagomorph species, but we found no credible associations. We attribute this discrepancy to the spatial scale of our analysis. Small mammals have much smaller home ranges than the carnivores we surveyed, and the 10-km buffers we used for describing fire history were probably not reflective of habitat conditions affecting the small mammals detected by our design of widely-dispersed cameras. Fine-scale habitat elements are particularly important for explaining the distribution of small mammals (Gray et al., 2016). For these reasons, we recommend further study of the effects of pyrodiversity on small mammals with a focus on the measurement of their abundances and the spatial patterning of fire at multiple spatial scales. This could involve evaluation of beta diversity instead of just the alpha diversity considered in our study (Farnsworth et al., 2014). This information would be useful for refining paired coarse and fine filter approaches to fire and forest management (DellaSala et al., 2017).

Allowing wildfires to burn across landscapes, either to increase biodiversity or for other reasons, poses a variety of challenges. Wildfires destroy homes and other property (Bryant & Westerling, 2014) and spread air pollution that negatively impacts human health (Cascio, 2018). These risks are magnified by the expansion of human development throughout California into forested landscapes (Hurteau et al., 2014). The policy of fire suppression, however, has exacerbated air pollution overall, whereas managed fire could mitigate human health impacts while restoring ecosystem services including improved wildlife habitat (Cisneros et al., 2017). Further, the increasing size of current high severity fires often retards post-fire forest regeneration (Haffey et al., 2018). Additionally, the effects of climate change and recent drought-induced tree mortality throughout large portions of the Sierra Nevada mountains are likely to alter the ecology of future forests in part by favouring regeneration of shade-tolerant species and further increasing the size of high severity fires (Stephens et al., 2018).

Considering the dual challenges of a changing climate and a human-dominated landscape, forest management can provide an alternative to wildfire in some situations (Allen et al., 2019). Prescribed burns in conjunction with mechanical treatments mimic some of the effects of wildfire and enhance wildlife habitat for small mammals (Amacher et al., 2008; Kalies et al., 2010). There is uncertainty on how these treatments can be best combined to improve habitat conditions for carnivores. There is concern that homogenously applied fuel treatments could adversely impact carnivore habitat (Hanson & Odion, 2016), especially in the short-term (Sweitzer et al., 2016), but also evidence that treatments can be designed in a way that do not negatively impact carnivores that use late-seral habitats (Zielinski et al., 2013). The strength of our results for short-term, low-severity
fire suggests that wildfire (or prescribed burning) may enhance wildlife habitat and provide other ecological services in a way that may be challenging to mimic using other forms of forest management.

In conclusion, we found evidence that an intermediate amount of fire severity diversity supports a high diversity of forest carnivores in California. Our optimization approach is similar to those taken by researchers from Australia for maximizing wildlife species richness using time-since-fire measurements in Eucalyptus-dominated woodlands (Di Stefano et al., 2013; Kelly et al., 2014). Our findings, however, apply specifically to fire severity diversity in the frequent-fire-adapted conifer forests of western North America. This difference highlights the importance of qualifying fire–wildlife inferences within the ecosystem context (Carbone et al., 2019; Geary et al., 2020). Additional study is required to evaluate whether the optimal conditions we identified hold across trophic levels. For example, results from Australia illustrated a difference in optimal fire conditions supporting vertebrates versus invertebrates (Di Stefano et al., 2013). Additional research is also important for elucidating whether maximizing species diversity (either alpha or beta diversity) reflects functional diversity leading to greater ecological resilience (Bukvareva, 2018), to improve understanding of the role of moderate severity fire, and for greater clarity about the extent to which forest management can be used to mimic the ecological role of wildfire. We also note that we found a range (0.32–0.76, 10 years) of fire severity diversity values that maximized occupancies of individual carnivore species. Although an intermediate level of fire severity diversity (e.g. 0.5) was optimal for overall species richness of carnivores, it was sub-optimal for the occurrence of either Western Spotted Skunk or Ringtail (Figure 3). Notwithstanding these caveats, a growing body of literature demonstrates the ecological and societal value of a mixed-severity fire regime and prescribed burning across much of California’s forested landscape (Stephens et al., 2020).

Detailed study of these biodiversity patterns and adaptively managing fire to better balance multiple ecological and social objectives will require a sustained commitment to long-term monitoring (Fernandez-Gimenez et al., 2008; Gonzales & Hoshi, 2015; Walters, 1986). Besides carnivores and their prey, recent study indicates that pyrodiversity is important for sustaining bird, bat, insect and plant populations in California (Ponisio et al., 2016; Steel et al., 2019; Tingley et al., 2016). Therefore, effective monitoring for informing conservation and management must address multiple taxa (Manley et al., 2005). Automated sensors including cameras and sound recorders combined with use of these data in multi-species occupancy modelling are an efficient means of obtaining this goal for numerous vertebrate species (Rich et al., 2019).

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at https://doi.org/10.6078/D1DT4S.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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