### RESEARCH ARTICLE



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# Wildfire disturbance and ecological cascades: Teasing apart the direct and indirect effects of fire on tick populations

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#### **Abstract**

- 1. Wildfires are a significant ecological force in the western United States, reshaping landscapes and ecological communities. However, assessing wildfires' full impact is challenging due to the complexity of fire severity and its varied effects on ecological dynamics. Understanding species-specific responses to disturbances within their environmental context is essential for predicting cascading ecological impacts. Arthropods, including ticks, are particularly sensitive to both abiotic and biotic changes, making them especially vulnerable to the impacts of wildfire.
- 2. In this study, we tease apart the complex direct and indirect effects of wildfire on tick populations through a combination of field-level measurements and remote sensing. We assessed tick densities across 88 plots within large, protected reserves in California following three wildfires in August 2020, using data on soil conditions, vegetation cover, tick densities and landscape-level remotely sensed variables related to vegetation regeneration and vertebrate recolonization. To support a multi-scalar approach, we applied piecewise structural equation models to incorporate factors across distinct spatial scales and assess how fire severity affects tick populations, with vegetation and habitat structure as mediating variables, thereby evaluating the relative importance of local drivers within a broader landscape context.
- 3. Our results indicate that tick densities were consistently lower in burned plots across all vegetation types, with higher fire severity associated with the greatest reductions. This direct effect of fire severity outweighed indirect influences such as the presence of remaining woody debris, which can support tick populations by offering microhabitat for vertebrate hosts following a fire event.
- 4. Landscape-level characteristics—such as proximity to the fire perimeter and the percentage of the reserve burned—exerted stronger influences on tick densities

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- than plot-level fire severity. These broader spatial characteristics likely facilitate the movement of vertebrate hosts into unburned areas, promoting tick recolonization and recovery following wildfire disturbance. Our results suggest that simplified field assessments focusing on key habitat indicators may be effective for monitoring tick responses to wildfire.
- 5. Synthesis and applications. This study highlights the importance of integrating multiple data sources and ecological scales to predict wildfire impacts on ecosystems and public health. By advancing our understanding of wildfire effects on ticks, the research offers valuable insights for ecosystem management and disease vector control. The use of advanced statistical tools, like piecewise structural equation models, combined with remotely sensed data, can facilitate rapid assessments and targeted monitoring efforts.

#### KEYWORDS

California wildfires, fire ecology, fire severity, structural equation modelling, tick ecology

#### 1 | INTRODUCTION

Wildfires are a key ecological force in the western United States, reshaping communities and ecosystems (Ayars et al., 2023; Jager et al., 2021; Schoennagel et al., 2017). However, the increasing frequency and severity of wildfires are outpacing the capacity of field-based studies to investigate their ecological impacts, necessitating greater reliance on remotely sensed data (Gibson et al., 2020; Saberi & Harvey, 2023; Wan et al., 2020). Keeping pace with the increasing frequency of wildfire is essential for accurately quantifying the impacts of fire on ecosystems, particularly as ecologists seek to understand the long-term effects of both natural and anthropogenically amplified fire regimes on ecological processes (Johnstone et al., 2016; Nimmo et al., 2022; Wintle et al., 2020).

To fully capture wildfire's effect on ecological communities, it is essential to move beyond simple unburned/burned classifications and instead consider multiple components of fire regimes, including fire intensity (heat energy released), burn extent (total area affected) and vegetation responses across diverse landscapes. While these elements are related, they capture distinct aspects of fire behaviour and impact. Among them, fire severity—which reflects the magnitude of ecological change, particularly to vegetation and soil—plays an important role in shaping post-fire ecosystem responses (Jones & Tingley, 2022; Keeley, 2009; Kobziar et al., 2024; Nimmo et al., 2022; Perry et al., 2011). Importantly, the ecological effects of fire severity, and other fire regime components, are not uniform: high heat intensity may benefit endemic plants adapted to fire-prone habitats, while harming invasive species and altering biodiversity (Keeley & Pausas, 2022). The size of the burned area can shape faunal community reassembly, influencing both intraspecific and interspecific competition (Jager et al., 2021; McLaughlin et al., 2022; Van Mantgem et al., 2015). Larger burns may lead to quicker recolonization by mobile species, like deer and birds, while smaller burns could see more intense competition as both mobile and less mobile species

recolonize at similar rates (Andrus et al., 2021; Calhoun et al., 2024; Diffendorfer et al., 2012; Van Mantgem et al., 2015). Furthermore, post-fire vegetation structure can influence the timing of species' return to burned areas where some species take advantage of open canopy, while others wait for shrub density to increase (Diffendorfer et al., 2012; Swan et al., 2015). The diverse and scale-dependent effects of fire severity complicate efforts to quantify wildfire's impact on ecological processes (Harrison et al., 2024).

Given the complexity of wildfire's effects on ecological communities, understanding species-specific responses to disturbances within their environmental context is crucial for predicting cascading ecological impacts (Albery et al., 2021; Grace & Keeley, 2006; Johnstone et al., 2016). Arthropods, including ticks, are highly sensitive to both abiotic and biotic shifts, making wildfires a key driver of population dynamics in fire-prone regions (Bieber et al., 2023; Holmquist et al., 2024; Pascoe et al., 2023). Ticks, as generalist feeders with life stage-specific habitat preferences, are integrated into complex multi-species communities (Castro & Wright, 2007; Padgett & Lane, 2001). Each life stage (larva, nymph, female adult) requires a blood meal from vertebrate hosts like rodents, birds and deer (Castro & Wright, 2007). The specific temperature and humidity thresholds for each stage influence their distribution across the landscape (Padgett & Lane, 2001). For example, larvae and nymphs, with less robust exoskeletons, are more prone to desiccation and tend to inhabit moist microhabitats like leaf litter under trees or shrubs, where humidity is higher and encounters with small hosts are frequent. In contrast, adult ticks are more resistant to desiccation and typically reside in taller grasses, where they encounter larger hosts, such as deer. These life stage-specific habitat preferences complicate efforts to quantify the overall impact of wildfire on tick populations. Previous studies on post-fire tick dynamics have produced mixed results (Gleim et al., 2014, 2019; MacDonald et al., 2018; Padgett et al., 2009; Pascoe et al., 2020, 2023), likely due to differences in fire severity and a limited focus on a subset of possible mechanisms.

To more effectively assess wildfire's impact on tick populations, it is essential to consider the complex interplay of physical factors—such as climate and soil—and biotic factors, including vegetation and vertebrate hosts. Due to this complexity, a more integrative approach is needed to understand how fire severity influences tick populations through its cascading effects on habitat, microclimates and ecological communities (Kobziar et al., 2024).

In California, wildfires affect diverse ecosystems, including grasslands, shrublands and conifer forests, with the severity of the fire's impact depending on the ecological context of each system (Calhoun et al., 2022; Coop, 2023; Roche et al., 2024; Steel et al., 2018). In landscapes with mixed vegetation, evaluating the overall impact of wildfire becomes even more complex, making it crucial to understand ecosystem-specific recovery processes and their downstream effects on ecological communities. While fire can destroy understory vegetation in forests, residual canopy cover after low- to moderate-severity burns may provide enough shade to reduce tick desiccation during the early post-fire period, before the understory regrows. In contrast, high-severity fires that remove the canopy crown can result in forest structures that resemble shrublands, potentially leading to comparable post-fire tick densities in both systems. Similarly, in grasslands, tick populations may remain relatively stable after low-intensity burns, as ticks can burrow into the soil to avoid high temperatures and vegetation often regrows rapidly enough to restore microclimatic conditions before desiccation. Variations in fire severity across these landscapes can lead to long-term shifts in ecosystem structure and function, influencing critical processes such as nutrient cycling, predator-prey interactions and food web resiliency (Doherty et al., 2022; McLaughlin et al., 2022; Pellegrini et al., 2020). Understanding these landscapespecific nuances is vital for assessing the broader impacts of wildfires, especially in the context of climate change (Jager et al., 2021; Kobziar et al., 2024; Van Mantgem et al., 2015).

In this study, we investigate the direct and indirect effects of fire severity on tick densities across 88 plots within large, protected reserves in California, following three independent wildfire events in August 2020. By combining local-level field data with landscapelevel remotely sensed data, we construct a quasi-causal network to explore the cascading effects of wildfire on tick populations. To evaluate the relative importance of various pathways, we employ piecewise structural equation models (SEMs), which are particularly suited for handling non-normal and spatially autocorrelated data within complex ecological networks (Lefcheck, 2016). Our focus is on both local conditions and broader spatial factors, including vegetation and potential vertebrate recovery rates, which may influence post-fire tick densities. We hypothesize that fire severity (1) directly affects tick densities through mortality, and (2) indirectly influences ticks by altering vegetation and habitat structures, which reduces microhabitat humidity, increases tick desiccation, and diminishes shelter for vertebrate hosts-critical blood meal sources for ticks. We explore these relationships in the context of reserve-specific characteristics, emphasizing vegetation regeneration and the potential recolonization of mobile hosts, as these factors may significantly

impact recovering tick populations. This study enhances our understanding of how wildfire severity influences tick populations and contributes to broader ecological processes, such as species recovery and ecosystem resilience (Kobziar et al., 2024). By examining the cascading effects of fire on ecological communities, this study helps predict long-term impacts on both ecosystem dynamics and public health, highlighting the importance of integrating diverse data sources and ecological scales in wildfire research.

#### 2 | MATERIALS AND METHODS

#### 2.1 | Wildfire events

In August 2020, an intense thunderstorm hit California, U.S.A., peaking at 200 lightning strikes in 30 min (Holmquist et al., 2024; Keeley & Syphard, 2021). Within 96 h, more than 12,000 lightning strikes sparked multiple fires around the northern California region, with some of these fires merging into the largest fire complexes in California history (CAL Fire, 2022) (Holmquist et al., 2024). Three of these fires impacted four large nature preserves in the University of California Natural Reserve System (UC NRS): McLaughlin Natural Reserve (LNU Lightning Complex, Hennessy Fire), Quail Ridge Reserve (LNU Lightning Complex, Hennessy Fire), Hastings Natural History Reservation (River Fire) and Landels-Hill Big Creek Reserve (Dolan Fire) (Figure 1).

#### 2.2 | Field-based data collection

#### 2.2.1 | Plot selection

Following the August wildfires, the UC NRS launched a rapid response team to assess the extent and severity of fire effects on protected ecosystems concentrated in the far-western region of California. A research team from the University of California, Santa Cruz, established a network of permanent plots across four reserves: McLaughlin Natural Reserve (ML; Lake County), Quail Ridge Reserve (QR; Napa County), Hastings Natural History Reservation (HT; Monterey County) and Landels-Hill Big Creek Reserve (BC; Monterey County). The goal was to create a long-term record of fire effects and vegetation responses, which could be linked with other ongoing studies and data collection (e.g. arthropods (Holmquist et al., 2024)) (Text S1). At each reserve, burned and unburned plots were selected across three dominant vegetation types-grassland, shrubland and forest. A total of 30 plots were targeted (15 per burn status, with 5 replicates per vegetation type). However, exceptions were made based on the extent of fire in different habitat types across the reserves sampled: Quail Ridge had only burned plots (n=15), and Big Creek lacked a full set of unburned grassland plots (n=23). Detailed sampling design and exceptions are provided in Table S1. To minimize environmental variability, plots were carefully selected to match conditions as closely as possible between burned and unburned areas, with attention given to maintaining

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FIGURE 1 Characterization of landscape conditions in the study region. (a) Wildfire perimeter from CAL FIRE, showing the overlap with four UC reserves. (b) Wildfire severity map for each UC reserve based on the differenced normalized burn ratio (dNBR) at 20 m resolution, derived from Sentinel-2 imagery. Fire severity was binned by numeric dNBR values.

consistent aspects within each vegetation type (e.g. shrubland on southerly aspects, forest on northerly aspects). Specific vegetation types (e.g. shrubland or chamise chaparral) and plot locations within each reserve are detailed in Figure S1. All plots were 10m diameter circles and separated by at least 40 meters.

#### 2.2.2 | Plot-level fire severity metrics

Within 3 months of the fire, plot-level assessments were conducted by a field team. To assess fire severity on the soil surface, each plot was classified into one of five fire severity categories: unburned, scorched (litter partially burned), lightly burned (litter charred but not fully consumed), moderately burned (litter mostly or entirely consumed) and heavily burned (litter and duff completely consumed). We use the soil surface severity category as our primary metric for assessing fire severity. For more detailed descriptions of the fire severity classifications, refer to Table S2.

#### 2.2.3 | Plot-level vegetation sampling

Vegetation assessments were made within 3 months of the fire (Fall 2020) and again during Spring 2021. To evaluate fire severity in terms of its effects on vegetation at a fine scale, we assessed the remaining live green vegetation and fuels at each plot, including the average diameter of coarse woody debris (cm) and the percentage of bare soil char. At 2 and 7 m from the plot center, the diameter of coarse woody debris

was estimated with a tape measure where each piece intersected the transect tape. The percentage of bare soil char was estimated based on ground-level observations and summed per plot. Additional details on variable measurements can be found in Table S3. No permits were required for the vegetation and soil sampling.

#### 2.2.4 | Tick sampling

A total of 88 unique plots were sampled for ticks across two seasons, with tick collection occurring on a subset of plots in 2021 (n=28)and the full set of plots in 2022 (n=88) (see Table S4 for sampling schedule). To capture the seasonality of all tick life stages (larvae, nymphs, adults) and optimize collection, sampling was conducted during the peak months of tick activity, from March through June each year (Table S5) (Sambado et al., 2024). This resulted in 250 sampling events (reserve-treatment-vegetation-replicate). At each sampled plot, an  $80 \,\mathrm{m}^2$  area was surveyed using traditional tick sampling methods with a  $1 \times 1 \,\mathrm{m}^2$  drag cloth (Salomon et al., 2020). Sampling began at the center of the plot and proceeded along eight transects in the cardinal (north, east, south, west) and intermediate (northeast, northwest, southeast, southwest) directions. After each transect, the drag cloth was lifted and checked for ticks. Collected ticks were removed with fine-tipped forceps and preserved in 70% ethanol for later identification in the laboratory. Tick counts were converted to density estimates (ticks per 100 m<sup>2</sup>) using the formula: tick density=(tick counts/ $80 \,\mathrm{m}^2$ )×100. Only plots suitable for tick populations were sampled; for example, shrubland areas on serpentine rock at McLaughlin were excluded due to their habitat unsuitability for ticks. Ticks were collected under California Department of Fish and Wildlife Scientific Collecting Permits (S-193220002-19357-001).

#### 2.3 | Remotely sensed data

Tick populations are shaped by both local and landscape factors, making it difficult to disentangle the relative contribution of each (MacDonald et al., 2022). To address this complexity, we integrated fine-scale, field-collected data with coarse-scale, remotely sensed measurements to capture variation across spatial scales. Plot-level factors were measured within a 10-m diameter sampling area and reflect immediate habitat conditions, while landscape-level factors were derived from remote sensing data aggregated at the UC reserve boundary. This multi-scalar approach enables us to evaluate the relative importance of local versus landscape drivers in shaping tick population dynamics following a wildfire.

#### 2.3.1 | Landscape-level fire perimeter metrics

To capture potential recolonization effects of mobile species moving from unburned to burned plots, we calculated (a) the percentage of area burned per reserve, and (b) the distance from plot centroid to

fire perimeter. After the focal fire event, we calculated the percentage of area burned per reserve using two spatial datasets: the historical California wildfire perimeter (CALFIRE FRAP) and UC reserve perimeter (UCNRS GIS) shapefiles. With the 'sf' package (Pebesma & Bivand, 2023), we calculated the percentage of reserve area burned as: (area of intersection/ total area of reserve) × 100. To calculate the distance from plot centroid to the edge of the fire perimeter, we used the st distance() function to calculate the Euclidean distance between the spatial features. We calculated the distance from each plot centroid to the nearest edge of the fire perimeter for both burned and unburned plots, under the assumption that proximity to the fire boundary influences vertebrate host movement. Specifically, we hypothesized that plots closer to the fire edge, whether within or outside the burn perimeter, would have a greater potential for host recolonization (in burned areas) or spillover (in adjacent unburned areas). To test this, we included an interaction between distance to fire perimeter and treatment status, expecting a steeper negative relationship in burned plots, where recolonization dynamics are more pronounced.

#### 2.3.2 | Landscape-level fire severity metrics

To visualize the potential impact of variability in fire severity within a UC reserve, we calculated the differenced normalized burn ratio (dNBR) using satellite imagery (Sentinel-2) at a 20-m resolution for each reserve (Figure 1) (Calhoun et al., 2024). Normalized burn ratio (NBR) is commonly used to estimate fire severity and is calculated by (NIR-SWIR)/(NIR+SWIR) (Keeley, 2009). A higher NBR signals healthier vegetation compared to a lower NBR. To calculate dNBR. an index that assesses relative change in dominant vegetation from pre- and post-fire images, for each reserve we downloaded satellite images pre-fire (2020-08-01) and post-fire (2020-10-01) and used the equation  $NBR_{prefire} - NBR_{postfire}$ . A higher dNBR signals higher fire severity compared to a lower dNBR. To classify fire severity for figures, we classified dNBR values as unburned (<0.1), low severity (0.1-0.26), moderate-low severity (0.27-0.43), moderate-high severity (0.44-0.65) and high severity (>0.66) using thresholds set by Key and Benson (2006). More details regarding image processing can be found in Text S2 and Table S6.

#### 2.3.3 | Vegetation recovery metrics

To evaluate vegetation before and after the wildfire, during the peak of tick seasonality, we calculated the Normalized Difference Vegetation Index (NDVI) using satellite imagery (Sentinel-2) for each plot centroid. Using remote sensing, we standardized vegetation measurements across all plots within the same time frame, enabling us to capture both pre-fire vegetation—difficult to assess at the plot level—and peak greenness during April, which coincides with peak tick seasonality. We downloaded Sentinel-2 imagery for each plot from three key time points: the spring prior to the fire (April 2020),

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the first spring post-fire (April 2021) and the second spring post-fire (April 2022). For each time point, we averaged 2–3 cloud-free images acquired during the month of April to generate representative monthly composites. We calculated NDVI using the equation NDVI<sub>prefire</sub> – NDVI<sub>postfire</sub> to compare the vegetation recovery rates between the first and second springs post-fire. Additional details can be found in Table S6.

#### 2.3.4 | Climate variability

Ticks spend most of their life span off host and exposed to the external environment, making them highly vulnerable to climate conditions. To account for climate variability across the UC reserves, we obtained data from the Parameter-elevation Regression on Independent Slopes Model (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data accessed 3 Jan 2025) with a spatial resolution of ~4 km, which was then extracted to the plot coordinates (Abatzoglou, 2013). We used a 30-year normal (1991–2020) for mean annual temperature (°C) and vapour pressure deficit (kPa) to account for long-term climate trends across the UC reserves. To capture short-term vegetation responses to precipitation, we included the average cumulative precipitation during the winter quarters (December-March) at the plot level, generating a winter-specific total for each plot per year. Specifically, we calculated the cumulative winter precipitation for the season preceding the fire (Winter 2019: December 2019-March 2020), the first winter post-fire (Winter 2021: December 2020-March 2021) and the second winter post-fire (Winter 2022: December 2021-March 2022) for each plot. Due to the ~4km spatial resolution of the climate data and the occurrence of multiple plots within the same grid cell, these variables primarily capture variation among UC reserves rather than fine-scale differences between individual plots within a reserve.

#### 2.4 | Statistical analysis

Our statistical analyses were designed to address three main objectives: (i) to build on prior tick-fire research by testing for overall effects of burn treatment on tick densities using a Wilcoxon ranksum test; (ii) to disentangle the direct and indirect pathways through which fire severity influences tick populations using piecewise SEMs; and (iii) to assess whether vegetation recovery rates differed among reserves using a paired Wilcoxon test.

#### 2.4.1 | Ticks

To assess whether fire influences tick densities and to facilitate comparison with previous tick-fire studies, we tested for differences in tick densities across burn treatments. We calculated tick density (ticks per 100 m²) with standard error for each burn treatment, vegetation type, year and reserve. A Wilcoxon rank sum test

was applied to compare tick density distributions in 2022 between burned and unburned plots, both across vegetation types and within each specific vegetation category. We focus on 2022 data because sampling that year was more systematic and consistent across all four UC reserves.

# 2.4.2 | Direct and indirect impacts of fire on tick populations

Wildfires have cascading effects on ecosystems, influencing multiple taxa and ecological processes in different ways that, in turn, may impact tick populations. These complex relationships were investigated using SEMs, which allow for the investigation of multiple different hypothesized pathways—for example, from fire through vegetation, microclimate and host habitat—and their relative strengths or contributions to tick densities (Grace et al., 2010; Grace & Keeley, 2006; Shipley, 1999). Given the non-normal distribution and spatial autocorrelation found in ecological data, piecewise SEMs (PSEMs) are particularly well suited to our analysis (Lefcheck, 2016). Unlike traditional SEMs, which fit a global model, PSEMs allow for the evaluation of individual path models (i.e. local estimation).

Based on prior studies of wildfire's effect on ticks (Gleim et al., 2014, 2019; MacDonald et al., 2018; Padgett et al., 2009; Pascoe et al., 2020, 2023), we hypothesized the following key pathways: (1) fire severity directly affects tick densities through burning and mortality, and (2) fire severity indirectly affects tick densities by reducing vegetation habitat. This reduction in vegetation can influence tick densities in two primary ways: increased fire severity leads to (a) an increase in bare soil char, which in turn lowers microhabitat humidity, exacerbating tick desiccation and (b) a decrease in coarse woody habitat, which limits habitat availability for vertebrate hosts (i.e. rodents, lizards) that ticks depend on for blood meals, thereby increasing tick mortality. We also sought to account for landscape-level factors that could influence climate suitability and the recolonization of key vertebrate hosts, thereby affecting plot-level tick densities following the wildfire. We hypothesized that (3) average climate factors—temperature and precipitation—could directly influence tick densities; (4) average climate factors could have affected the percentage of the reserve burned (e.g. higher temperatures and more winter precipitation may contribute to a greater percentage of the reserve being burned); and (5) plot-level fire severity metrics may be influenced by the distance from plots to fire perimeter, with plots located further within the burn areas hypothesized to experience higher fire severity. This expectation is based on the tendency for fire behaviour to be less intense near perimeter edges where suppression efforts (e.g. back burning, establishment of handlines and dropping of fire retardant) are concentrated and more intense farther from perimeter edges where fuel continuity is greater. However, we recognize that this relationship is a generalization and in reality can vary dramatically depending on local topography, weather conditions and fuel structure (Parkins et al., 2018). We further hypothesize that this relationship may be strengthened in reserves where a greater percentage of the area was burned, reflecting more extreme or continuous fire spread.

To explore the direct and indirect effects of fire severity on tick densities (measured as ticks per 100 m<sup>2</sup>), we built PSEMs incorporating these pathways incorporating data from both 2021 and 2022. We first built a plot-level model to identify key characteristics of local effects on tick densities. Plot-level predictors included field-measured fire severity of surface soil (0-5 scale, with 0 representing unburned and 5 indicating high severity), the percentage of bare soil char and the average diameter of coarse woody debris. The percentage of bare soil char represents the pathway linked to microhabitat humidity, while the coarse woody debris represents the pathway linked to shelter for vertebrate blood meals. Understanding that plot-level conditions are shaped by landscape-level factors, we developed a separate landscapelevel model to examine how vertebrate recolonization rates from unburned to burned plots are influenced (Grace & Keeley, 2006). This model incorporates variables such as the distance from the plot centroid to the fire perimeter and the percentage of the reserve area that burned. To account for the influence of climate on post-fire dynamics and tick populations, particularly through effects of vegetation recovery, we included key climate variables in our landscape-level model. Specifically, we incorporated temperature normal and recent cumulative winter precipitation. To isolate the distinct roles of precipitation, we modelled separate paths for its effects: (i) pre-fire precipitation (Winter 2020) was hypothesized to influence the percentage of the reserve burned, while (ii) post-fire precipitation (Winters 2021 and 2022) was expected to affect post-fire tick densities by shaping vegetation recovery conditions. After assessing the local- and landscape-level effects on tick densities, we developed a comprehensive model that incorporates all the variables mentioned above (i.e. the inclusive model).

Unlike traditional SEMs, piecewise SEMs use local estimation, which requires developing a specific equation for each pathway. Given the hierarchical structure of the data, including repeated measurements of tick densities across plots, we first fit individual path models using the random effect structure with the Imer() function from the 'Ime4' package (Bates et al., 2015). Depending on the structure of each individual path model, we incorporated different random effects, such as reserve, treatment or vegetation category, to account for variation at appropriate hierarchical levels. For example, in the woody debris path model, we included vegetation category as a random effect, based on the assumption that grasslands contain less woody debris than forests prior to fire. This approach allowed us to better account for baseline differences in structural habitat features across vegetation types when modelling fire-related effects. After fitting individual paths and checking for normality assumptions, we applied the models to the psem() function from the 'piecewiseSEM' package (Lefcheck, 2016). Model fit was evaluated using Fisher's C statistic, and we compared nested models using AIC. Models with a  $\Delta$ AIC>2 were considered distinguishable. For each model, we report standardized coefficients for individual paths and estimate indirect effects through coefficient multiplication. To visualize SEM results we use the semPaths() function from the 'semPlot'

package (Epskamp et al., 2022). See Text S3 for additional data cleaning justifications and Text S4 for full model pathways.

#### 2.4.3 | Vegetation recovery/mechanism

We hypothesize that ticks surviving the fire depend on sufficient vegetation cover to reduce desiccation risk, and that post-fire vegetation regrowth facilitates the return of vertebrate hosts necessary for future tick blood meals. To assess vegetation recovery and better understand the temporal trends of tick densities, we performed a Wilcoxon signed-rank test comparing the Normalized Difference Vegetation Index (NDVI) before (1 April 2020) and after (4 April 2021) the fire for each burned plot (e.g. QR-Burn-G-01). This paired test accounted for vegetation types in the NDVI calculation, though we tested each reserve separately. We performed a similar analysis using the dNBR.

#### 2.4.4 | Software

All statistical analyses were conducted in RStudio version 4.4.1 (R Core Team, 2024), with a significance level set at p < 0.05. Data cleaning and visualization were conducted with 'tidyverse' and 'ggplot2' packages, respectively (Wickham, 2016; Wickham et al., 2019). The analysis was conducted using the following R package versions: ggplot2\_3.5.2, lme4\_1.1-35.3, piecewiseSEM\_2.4.0.1, semPlot\_1.1.6, sf\_1.0-20, tidyverse\_2.0.0. A list of data sources used in this study is provided in the Data Sources section.

#### 3 | RESULTS

#### 3.1 | Tick collection summary

A total of 449 ticks were collected post-fire, with over 90% of them being adults. Averaged across our study, unburned plots had higher tick densities (mean ± standard error, 4.18 ± 0.7) than burned plots  $(1.00\pm0.2)$  (Table 1). When plots were aggregated to dominant vegetation type across all reserves, in unburned treatments, shrubland had the highest density of ticks per  $100 \,\mathrm{m}^2$  (5.10 ± 1.6), followed by forest (4.88 $\pm$ 1.1) and grassland (2.58 $\pm$ 1.2) (Figure 2). In burned treatments, forest had the highest density of ticks  $(1.17 \pm 0.3)$ , followed by shrubland (0.94 $\pm$ 0.4) and grassland (0.83 $\pm$ 0.2). On burned plots, 2021 had a higher density of ticks (1.22±0.3) than 2022 (0.91  $\pm$  0.2), suggesting an indirect effect of fire on tick densities (Figure S2). Reserve-specific mean tick densities can be found in Table 2. The Wilcoxon rank-sum test revealed a significant difference in the distribution of tick densities sampled from 2022 between burned and unburned plots (W = 2432, p-value < 0.001). For specific vegetation types in 2022, there was a significant difference between burned and unburned plots in shrubland (W=189.5, p-value=0.02)

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					Mean tick density (SE)	
Reserve	Temp	VPD	Precip	% Burned	Unburn	Burn
McLaughlin (ML)	15.40	12.90	79.04	49.69	$3.01\pm1.0$	$1.64 \pm 0.4$
Quail Ridge (QR)	15.69	11.30	58.69	97.97	NA	$0.07 \pm 0.0$
Hastings (HT)	14.30	10.80	80.97	20.73	$5.89 \pm 1.4$	$1.93 \pm 0.5$
Big Creek (BC)	13.93	6.56	108.23	91.49	$2.76 \pm 0.8$	$0.36 \pm 0.2$

Note: Temperature (temp, °C) and vapour pressure deficit (VPD, kPa) represent the 30-year normals of annual mean. Precipitation (precip, mm) represents the average cumulative precipitation per rain season during our study period.

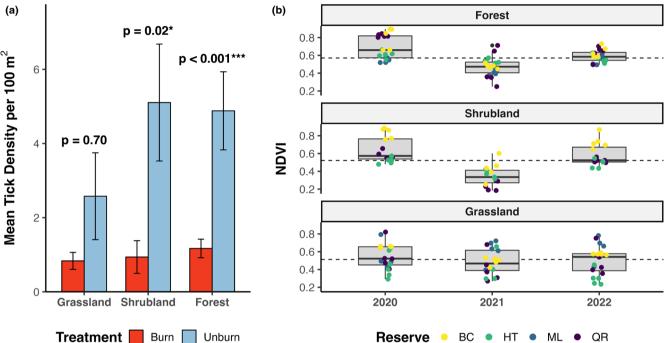


FIGURE 2 Post-fire dynamics of vegetation and tick populations at UC reserves. (a) Tick densities (per 100 m<sup>2</sup>) by reserve and vegetation type, colour-coded by burn treatment. Error bars represent standard errors. p-values are from Wilcoxon rank-sum test for 2022 samples between burned and unburned vegetation plots. (b) Normalized Differenced Vegetation Index (NDVI) values from Sentinel-2 for all burned plots, with data colour-coded by reserve. The dashed line represents the pre-fire median NDVI for each habitat type. NDVI measurements were taken annually in the first week of April (see Table S6 for dates). Asterisks indicate significances: \*\*\* $p \le 0.001$ , \* $p \le 0.005$ .

TABLE 2 Mean tick densities (with standard error) by treatment, reserve and vegetation type.

		Dominant vegetation type		
Treatment	Reserve	Grassland	Shrubland	Forest
UNBURN	ML	$0.9\pm0.5$	NA	$5.1\pm1.9$
	QR	NA	NA	NA
	HT	$4.2\pm2.2$	$10.2\pm3.1$	$4.8\pm1.9$
	ВС	NA	$1.4\pm0.6$	$4.6\pm1.7$
BURN	ML	$1.1\pm0.4$	NA	$2.1\pm0.6$
	QR	$0\pm0$	$0.1\pm0.1$	$0.1\pm0.1$
	HT	$1.6\pm0.6$	$2.2\pm1.4$	$2.1\pm0.6$
	ВС	$0.4 \pm 0.2$	$0.6 \pm 0.4$	$0.1\pm0.1$

Note: Reserve names are McLaughlin (ML), Quail Ridge (QR), Hastings (HT) and Big Creek (BC).

and forest (W = 246, p-value < 0.001) vegetation types, but no significant difference in grassland (W=380, p-value=0.70).

#### Wildfire characteristics at the reserve level

The percentage of burned area per reserve was highest at Quail Ridge Reserve (97.97%), followed by Landels-Hill Big Creek Reserve (91.49%), McLaughlin Natural Reserve (49.69%) and Hastings Natural History Reservation (20.73%) (Table 1). The distance from unburned plots to fire perimeters was lowest at Landels-Hill Big Creek Reserve (mean  $\pm$  standard error, 87.19  $\pm$  21.2 m), followed by Hastings Natural History Reservation (258.34±41.2m) and McLaughlin Natural Reserve (629.88 $\pm$ 113.2m) (Figure S3). Variation in long-term (30year normals) and short-term (during study period) climate variables across the reserves can be found in Figure S4.

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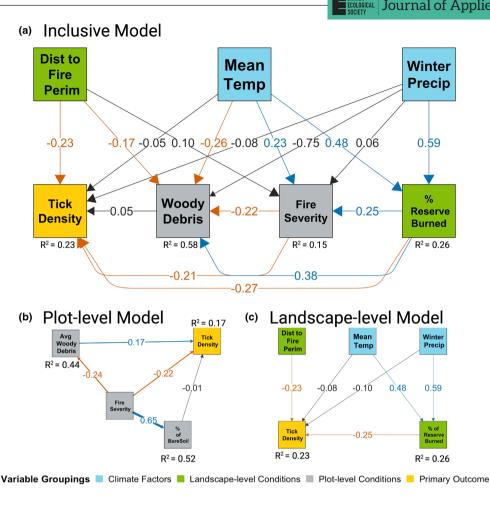


FIGURE 3 The best fit piecewise structural equation models for (a) the main, inclusive model, (b) plot-level model, (c) landscape-level model. Standardized regression coefficients are displayed and colour-coded for negative (red), positive (blue) and non-significant (grey) path results (p > 0.05).  $R^2$  values are included for each path model. Square boxes are colour-coded for variable groupings.

#### 3.3 **SEM results**

We applied piecewise SEMs to test the direct and indirect effects of fire severity on tick densities per plot (Figure 3). The inclusive model with both plot- and landscape-level conditions was an adequate fit to the data based on Fisher's C statistic ( $C_2 = 4.26$ , p-value = 0.10), with significant direct and indirect effects on tick densities. The greatest direct effects on tick densities were the percentage of the reserve burned (standardized coefficient=-0.27, p-value<0.001), distance from plot centroid to fire perimeter (standardized coefficient = -0.23, p-value < 0.001) and soil surface fire severity (standardized coefficient = -0.21, p-value = 0.001). Variance inflation factor analysis indicated high collinearity among the three winter precipitation variables (pre-fire, post-fire year 1 and post-fire year 2). To address this and reduce multicollinearity in the model, we averaged precipitation across all three winters to generate a single composite variable representing overall winter precipitation for each reserve (i.e. average cumulative winter precipitation). The cumulative winter precipitation served as a general proxy for regional precipitation patterns over the study period. Indirectly, mean temperature and cumulative winter precipitation had an effect on tick densities, with

the strongest path mediated by the percentage of reserve burned (standardized coefficient = -0.11 for temperature, standardized coefficient=-0.13 for precipitation). The landscape-level ( $C_2=4.62$ , p-value=0.10) and plot-level ( $C_2$ =2.34, p-value=0.31) models also fit the data sufficiently. To note, in the plot-level model, the average coarse woody debris had a significant direct effect on tick densities (standardized coefficient=0.17, p-value=0.03) but was insignificant in the full model that contained landscape-level effects (i.e. inclusive model). Additional pathway results, including results from the full model (landscape and local conditions), can be found in Table S7.

#### Vegetation recovery rate

The Wilcoxon signed-rank tests indicated that some reserves had significantly different NDVI values between pre-fire and post-fire, suggesting that vegetation was significantly different after fire, which was expected and represented by a decreased NDVI value (Table 3; Figure 2). Reserves that had significant differences of NDVI values in the first springcompared to pre-fire spring-indicating significant differences in vegetation post fire—were Quail Ridge (V=0, p-value < 0.001),

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TABLE 3 Wilcoxon signed-rank test comparing post-fire NDVI to pre-fire NDVI for paired burned plots.

Reserve	Pre-fire vs. 1st year spring	Pre-fire vs. 2nd year spring
ML	p-value = 0.43 (V = 19)	p-value=0.70 (V=32)
QR	p-value = <0.001 (V=0)***	p-value = <0.001 (V=1)***
HT	p-value=0.002 (V=8)**	p-value = <0.001 (V=1)***
ВС	p-value=0.001 (V=0)**	p-value=<0.001 (V=0)***

Note: NDVI values were downloaded from the first week of April in 2020 (pre-fire), in 2021 (1st year spring) and in 2022 (2nd year spring). The V statistic reflects the rank sum of differences between post-fire and pre-fire NDVI values. A V value of 0 indicates that NDVI is higher in pre-fire than post-fire. Reserve names are: McLaughlin (ML), Quail Ridge (QR), Hastings (HT) and Big Creek (BC). Asterisks indicate significances: \*\*\* $p \le 0.001$ , \*\* $p \le 0.01$ .

Big Creek (V=0, p-value < 0.001) and Hastings (V=8, p-value = 0.002). The vegetation differences from pre- and post-fire were not significantly different at McLaughlin for Spring 2021 (V=19, p-value = 0.4) or Spring 2022 (V=32, p-value = 0.70) (Figure S5). Our results for NBR, which showed similar patterns, are reported in Table S7.

#### 4 | DISCUSSION

Understanding how wildfires affect arthropod vectors, such as ticks, is inherently challenging due to the complex interplay between these organisms, their vertebrate hosts and the environment. Factors such as long life cycles, habitat-host preferences, and the numerous direct and indirect pathways through which both local- and landscape-level elements influence tick populations further complicate this task. The variability in fire severity across heterogeneous landscapes only adds another layer of complexity. In this study, we adopt a novel approach by examining the impact of three wildfires that occurred in August 2020, spanning multiple vegetation types and regions in California. By incorporating both local- and landscape-level characteristics of fire severity, we explore how these factors shape tick populations through a range of direct and indirect mechanisms. Our primary findings reveal that: (1) increased fire severity directly reduces tick densities, (2) landscape-level factors, such as distance from the fire perimeter and the percentage of reserve burned, have significant and negative effects on tick populations, which we hypothesize reflect the potential for mobile host recolonization from unburned to burned areas, (3) burned plots generally exhibit lower tick densities, although this pattern is influenced by vegetation type, with forests showing a significantly larger difference in tick densities between unburned and burned plots. Through this integrative approach combining field data, remote sensing and modelling, we aim to clarify how wildfires influence tick populations through both direct and indirect pathways, offering valuable insights for future research and ecological monitoring in fire-prone ecosystems facing increasingly frequent and severe wildfires.

Earlier studies on the effect of wildfire on tick populations have reached opposing conclusions, with varying methods of measuring

wildfire impacts and differing ecological contexts. Some research has focused on prescribed burns (Gleim et al., 2014, 2019; Padgett et al., 2009), while others have examined the consequences of wildfires (MacDonald et al., 2018; Pascoe et al., 2020, 2023). In prescribed burns, there was not always a significant difference in questing tick abundance between burned and unburned plots, possibly due to the lower heat intensity and perimeter size typically associated with prescribed fires (Padgett et al., 2009). From our SEMs, we found that increased fire severity reduced tick densities, likely because more intense fire penetrates deeper into soil refugia, which may protect ticks in lower-severity fires (Padgett et al., 2009). Higher levels of soil heating can influence post-fire recovery dynamics where an increase in heat can have lasting effects on the soil itself, altering its chemistry, structure and microbiome, all of which can have negative influence on vegetation recovery and thus ticks. Additionally, previous studies have targeted different vegetation types, including grasslands (Goodenough et al., 2017), chaparral (Padgett et al., 2009) and oak woodland/forests (MacDonald et al., 2018, Pascoe et al., 2020, 2023), each with distinct fire ecologies (Calhoun et al., 2022). Our study adds a unique perspective by examining the effect of wildfires across four distinct regions and multiple dominant vegetation types, allowing us to explore how wildfire influences tick populations across different ecosystems. We found that burned plots generally had lower tick densities than unburned plots within 2 years post-fire, a result that aligns with some studies (Pascoe et al., 2020) but contradict others (MacDonald et al., 2018). This discrepancy may be attributed to differences in vegetation types, local ecological factors, or fire severity. Specifically, we found that burned plots in forests had higher tick densities compared to shrublands and grasslands. This could be due to the structural characteristics of forests remaining after low-severity fires-such as denser vegetation and greater shade-which provide better protection from desiccation and create more favourable habitats for vertebrate hosts, crucial for tick survival (Pascoe et al., 2023). Conversely, in the grassland sites we see no observable difference in tick densities or NDVI values likely because the grasslands of this region are primarily composed of annual and fast-growing perennial species, compared to shrublands and forest. Although we did not directly measure vertebrate host abundance, we used coarse woody debris as a proxy for potential host presence. Other studies have shown that plots with more woody debris or less disturbed habitats tend to support higher numbers of mammals, including the duskyfooted woodrat, a key host for ticks (MacDonald et al., 2018; Pascoe et al., 2020, 2023). These findings suggest that the availability of suitable hosts and habitat structure likely plays a crucial role in shaping tick populations following wildfire, and further research on host dynamics in burned and unburned areas would be valuable to better understand these interactions.

The mechanisms through which fire severity influences tick populations are multifaceted, and our study identifies several key factors. Although our plot-level SEM suggested that increased coarse woody debris could enhance tick densities, our inclusive SEM model highlighted the importance of broader landscape context. Factors such as distance to the fire perimeter (standardized

coefficient = -0.27, p-value < 0.001) and the percentage of the reserve burned (standardized coefficient = -0.23, p-value < 0.001) emerged as stronger direct influences on tick densities than plot-level fire severity (standardized coefficient = -0.21, pvalue = 0.001). Specifically, as the distance from the fire perimeter and the percentage of burned area increased, tick densities tended to decrease. From our additional analysis (Text S5), we find that the negative relationship is driven primarily by unburned plots, where tick densities are higher closer to the fire perimeter and decline with increasing distance for unburned plots. This pattern may reflect the spillover of mobile hosts, such as birds and deer, migrating from burned to unburned areas, which could aid in tick population recovery. Although this is an interesting finding, the relationship between tick densities and distance to the fire perimeter should be further evaluated with targeted field collections. In general, community reassembly is contingent upon the rate of vegetation regeneration and the availability of suitable habitat outside the fire perimeter, which will be spatially and temporally context dependent (Van Mantgem et al., 2015).

Interestingly, while we hypothesized that climate variables like annual mean temperature and cumulative winter precipitation would directly impact tick densities, our SEM results showed no significant direct effects of these variables on tick populations, possibly due to the coarse scale of our evaluation, which micro-habitat data loggers could better address. However, both climate factors did indirectly affect tick populations through the percentage of the reserve that burned (temperature indirect standardized coefficient = -0.16; precipitation indirect standardized coefficient = -0.13). Specifically, reserves with higher average annual temperatures and greater cumulative winter precipitation tended to have larger areas burned (temperature standardized coefficient = 0.48; precipitation standardized coefficient = 0.59). This observation may be linked to the increasing hydroclimatic variability California has experienced in recent years and linked to other large-scale wildfires (Swain et al., 2025), as these conditions can intensify fire behaviour and burn severity. The reserves with the highest burn percentage-Quail Ridge (~97%) and Big Creek (~91%)-showed notable differences in vegetation recovery, as indicated by significant changes in NDVI and dNBR, particularly in the second spring post-fire (April 2022), when tick sampling occurred. In contrast, reserves like McLaughlin (~49% burned) and Hastings (~20% burned) showed less pronounced vegetation differences pre- and post-fire. These landscape characteristics likely explain why our landscape-inclusive SEM model ( $R^2 = 0.23$ ) accounted for more variation in tick densities than the plot-only model ( $R^2$  = 0.17). However, it is important to acknowledge that our SEM models have relatively low explanatory power, and we encourage future research to refine these models by incorporating additional factors, such as the historical wildfire regime and tick population dynamics at each reserve, to improve the robustness of predictions. Future analyses could benefit from a more spatially nuanced approach—such as calculating the percentage of burned areas within concentric buffers around each plot-to

better capture gradients of landscape influence and potential host movement patterns. Integrating both field-collected and remotely sensed data remains a challenge, but advancing this integration could improve the scalability and accuracy of wildfire impact studies, offering valuable insights into ecosystem management strategies in the context of global change (Gibson et al., 2020; Saberi & Harvey, 2023).

While our study offers valuable insights into the effects of wildfire on tick populations, several limitations should be noted. Accurately measuring fire severity is inherently complex, but doing so is critical for capturing the nuanced ecological responses to fire. Our plot-level fire severity assessment, while less rigorous than established metrics such as the Composite Burn Index (BCI; Key & Benson, 2006), offers a practical and scalable alternative for comparing conditions across many plots within a limited timeframe. We believe this index represents a meaningful improvement over simple binary classifications of burned versus unburned areas. However, the effectiveness of our fire severity metric could have been enhanced by more balanced representation across the full severity spectrum, particularly at the lower end (severity levels 1 and 2, indicating scorched or lightly burned conditions). This uneven distribution may limit our ability to detect subtle ecological responses to low severity burns and could bias our findings towards patterns associated with moderate to high fire severity. We also acknowledge that using woody debris as a proxy for vertebrate presence is an imperfect assumption. This limitation could have been addressed by incorporating camera traps at our plots to directly monitor vertebrate activity. Temporal data on the return of mobile hosts, such as deer and birds, would have provided valuable context for interpreting landscape-level metrics like distance to the fire perimeter and percentage of reserve burned. These data would have allowed for a more explicit assessment of postfire community reassembly-a process known to follow diverse trajectories in biodiversity-rich regions (McLaughlin et al., 2022; Pascoe et al., 2020; Van Mantgem et al., 2015). While it was beneficial that all wildfires occurred in August, enabling more consistent comparison across reserves, we note that tick activity is generally low at this time, which limits our ability to assess immediate fire impacts. This seasonal mismatch may obscure short-term responses in tick populations. Extending the temporal scope of tick sampling to encompass a full life cycle (approximately 3 years) post-fire would offer a more comprehensive understanding of population dynamics, including potential lag effects and variation across life stages (Bieber et al., 2023). In sum, while our study offers an important step in the wildfire-tick literature, future work has many opportunities to refine and expand upon this foundation, as the ecological consequences of wildfire are complex and multifaceted.

As wildfire events increase in frequency and severity, outpacing the capacity of field-based monitoring, linking on-the-ground data with remote sensing is becoming not only a promising avenue of research but also a necessary strategy for effective ecological monitoring and management. However, the ecological effects

of fire are highly context-dependent and often difficult to generalize, requiring integrative, hypothesis-driven approaches that can bridge spatial and temporal scales. Piecewise SEMs provide a powerful framework for integration and comparison of the various components that are part of ecosystems. Our study demonstrates how integrative modelling can build upon prior knowledge to streamline future data collection and improve predictive capacity in post-fire landscapes. We propose ticks are useful indicator species for monitoring ecosystem responses to wildfire, given their connectedness to both abiotic (e.g. vegetation structure, microclimate) and biotic (e.g. host availability) components of the environment. Ticks are relatively easy and cost-effective to sample across a range of habitats in the western U.S.A., requiring minimal equipment and permitting compared to more logistically demanding taxa such as rodents, birds or large mammals. This practicality makes ticks a strong candidate for use in long-term monitoring programmes, particularly in fire-prone systems where rapid assessment is critical. By selecting indicator species that are ecologically informative yet logistically feasible to monitor-and pairing them with robust, multi-scale statistical tools—we can improve our ability to assess ecosystem recovery and guide adaptive management in landscapes increasingly shaped by wildfire.

Our findings carry several important management implications for a wide range of stakeholders. First, as the use of prescribed fire, or 'good fire', continues to expand across California as a costeffective strategy for reducing fuel loads and controlling invasive species, our research highlights an additional public health benefit: the potential to reduce tick populations, and in turn, tick-borne disease risk. This is particularly relevant in regions where tick-borne pathogens are common, such as the northern coastal areas and Sierra foothills. However, our results indicate that the effectiveness of prescribed fire in reducing tick populations is strongly influenced by both vegetation type and fire severity. Specifically, we found that fire is most effective in shrublands and least effective in forested areas. Second, our research demonstrates the value of using tick populations as a multi-dimensional indicator of post-fire ecosystem recovery. Because tick density can reflect the regrowth of vegetation and the return (or absence) of wildlife hosts, monitoring tick populations, especially with pre-fire baseline data, offers a promising tool for assessing ecological recovery. This approach is especially timely, as California faces increasingly frequent, severe and expansive wildfires with complex, long-term ecological impacts that land managers and researchers, much account for.

#### 5 | CONCLUSIONS

Our study highlights the complex, multi-scale interactions between wildfire and tick populations, showing how fire severity, vegetation type and landscape context collectively shape tick densities in post-fire environments. While we identify clear direct effects of fire severity, a deeper understanding will require incorporating host dynamics and expanding long-term monitoring. Future research should

prioritize multi-year sampling to capture full tick life cycles, integrate tools such as camera traps to track vertebrate hosts, and include controls such as climate variability and fire history to improve predictive models. By combining field-based sampling with scalable remote sensing and integrative modelling, this research offers a practical framework for monitoring post-fire ecological change. Using ticks as a cost-effective indicator species provides a feasible strategy for assessing ecosystem recovery across fire-prone land-scapes. Ultimately, our findings inform both ecological theory and applied efforts to manage public health risks and biodiversity in an era of increasingly frequent and severe wildfires.

#### **AUTHOR CONTRIBUTIONS**

Samantha Sambado conceived the idea for this project, collected the tick field data, conducted the analysis and wrote the original draft of the manuscript. Gage Dayton and Kelly M. Zilliacus contributed to the field study design and maintained the database for the vegetation surveys. Samantha Sambado, Gage Dayton, Kelly M. Zilliacus, Shane Dewees, Andrew J. MacDonald and Cheryl J. Briggs contributed to the manuscript drafts and approved the final version for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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#### DATA AVAILABILITY STATEMENT

Remotely sensed data are freely available online and links can be found in the Data Sources section, as well as in Table S8. The data and code to re-create figures and analysis are stored via Dryad Digital Repository (https://doi.org/10.5061/dryad.41ns1rnt4) (Sambado et al., 2025) and can also be found on GitHub (https://github.com/sbsambado/ucnrs\_wildfire).

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#### REFERENCES

- Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, 33, 121–131.
- Albery, G. F., Turilli, I., Joseph, M. B., Foley, J., Frere, C. H., & Bansal, S. (2021). From flames to inflammation: How wildfires affect patterns of wildlife disease. *Fire Ecology*, *17*, 23.
- Andrus, R. A., Martinez, A. J., Jones, G. M., & Meddens, A. J. H. (2021).
  Assessing the quality of fire refugia for wildlife habitat. Forest Ecology and Management, 482, 118868.
- Ayars, J., Kramer, H. A., & Jones, G. M. (2023). The 2020 to 2021 California megafires and their impacts on wildlife habitat. *Proceedings of the National Academy of Sciences of the United States of America*, 120, e2312909120.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bieber, B. V., Vyas, D. K., Koltz, A. M., Burkle, L. A., Bey, K. S., Guzinski, C., Murphy, S. M., & Vidal, M. C. (2023). Increasing prevalence of severe fires change the structure of arthropod communities: Evidence from a meta-analysis. Functional Ecology, 37, 2096–2109.
- Calhoun, K. L., Chapman, M., Tubbesing, C., McInturff, A., Gaynor, K. M., Van Scoyoc, A., Wilkinson, C. E., Parker-Shames, P., Kurz, D., & Brashares, J. (2022). Spatial overlap of wildfire and biodiversity in California highlights gap in non-conifer fire research and management. *Diversity and Distributions*, 28, 529–541.
- Calhoun, K. L., Connor, T., Gaynor, K. M., Van Scoyoc, A., McInturff, A., Kreling, S. E. S., & Brashares, J. S. (2024). Movement behavior in a dominant ungulate underlies successful adjustment to a rapidly changing landscape following megafire. Movement Ecology, 12, 53.
- Castro, M. B., & Wright, S. A. (2007). Vertebrate hosts of Ixodes pacificus (Acari: Ixodidae) in California. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 32, 140–149.
- Coop, J. D. (2023). Postfire futures in southwestern forests: Climate and landscape influences on trajectories of recovery and conversion. *Ecological Applications*, 33, e2725.
- Diffendorfer, J., Fleming, G. M., Tremor, S., Spencer, W., & Beyers, J. L. (2012). The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral. *International Journal of Wildland Fire*, 21, 436.
- Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., Cherry, M. J., Conner, L. M., González, T. M., Legge, S. M., Ritchie, E. G., Stawski, C., & Dickman, C. R. (2022). Fire as a driver and mediator of predator-prey interactions. *Biological Reviews*, 97, 1539-1558.
- Epskamp, S., Stuber, S., Nak, J., Veenman, M., & Jorgensen, T. (2022). semPlot: Path diagrams and visual analysis of various SEM packages' output.
- Gibson, R., Danaher, T., Hehir, W., & Collins, L. (2020). A remote sensing approach to mapping fire severity in south-eastern Australia using

- sentinel 2 and random forest. Remote Sensing of Environment, 240, 111702.
- Gleim, E. R., Conner, L. M., Berghaus, R. D., Levin, M. L., Zemtsova, G. E., & Yabsley, M. J. (2014). The phenology of ticks and the effects of Long-term prescribed burning on tick population dynamics in southwestern Georgia and northwestern Florida. PLoS One, 9, e112174.
- Gleim, E. R., Zemtsova, G. E., Berghaus, R. D., Levin, M. L., Conner, M., & Yabsley, M. J. (2019). Frequent prescribed fires can reduce risk of tick-borne diseases. Scientific Reports, 9, 9974.
- Goodenough, A. E., Harrell, A. N., Keating, R. L., Rolfe, R. N., Stubbs, H., MacTavish, L., & Hart, A. G. (2017). Managing grassland for wildlife: The effects of rotational burning on tick presence and abundance in African savannah habitat. *Wildlife Biology*, 2017, 1–8.
- Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80, 67–87.
- Grace, J. B., & Keeley, J. E. (2006). A structural equation model analysis of Postfire plant diversity in California Shrublands. *Ecological Applications*, 16, 503–514.
- Harrison, M. E., Deere, N. J., Imron, M. A., Nasir, D., Adul, Asti, H. A., Aragay Soler, J., Boyd, N. C., Cheyne, S. M., Collins, S. A., D'Arcy, L. J., Erb, W. M., Green, H., Healy, W., Hendri, Holly, B., Houlihan, P. R., Husson, S. J., Iwan, ... Struebig, M. J. (2024). Impacts of fire and prospects for recovery in a tropical peat forest ecosystem. Proceedings of the National Academy of Sciences of the United States of America, 121, e2307216121.
- Holmquist, A. J., Cody Markelz, R. J., Martinez, C. C., & Gillespie, R. G. (2024). The importance of habitat type and historical fire regimes in arthropod community response following large-scale wildfires. *Global Change Biology*, 30(1), e17135. https://doi.org/10.1111/gcb.17135
- Jager, H. I., Long, J. W., Malison, R. L., Murphy, B. P., Rust, A., Silva, L. G. M., Sollmann, R., Steel, Z. L., Bowen, M. D., Dunham, J. B., Ebersole, J. L., & Flitcroft, R. L. (2021). Resilience of terrestrial and aquatic fauna to historical and future wildfire regimes in western North America. Ecology and Evolution, 11, 12259–12284.
- Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment, 14, 369–378.
- Jones, G. M., & Tingley, M. W. (2022). Pyrodiversity and biodiversity: A history, synthesis, and outlook. *Diversity and Distributions*, 28, 386-403.
- Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, 18, 116.
- Keeley, J. E., & Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics*, 53, 203–225.
- Keeley, J. E., & Syphard, A. D. (2021). Large California wildfires: 2020 fires in historical context. Fire Ecology, 17, 22.
- Key, C. H., & Benson, N. C. (2006). Landscape assessment: Ground measure of severity, the Composite Burn Index; and remote sensing of severity, the Normalized Burn Ratio. In D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Benson, S. Sutherland, & L. J. Gangi (Eds.), FIREMON: Fire effects monitoring and inventory system (Gen. Tech. Rep. RMRS-GTR-164). US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Kobziar, L. N., Hiers, J. K., Belcher, C. M., Bond, W. J., Enquist, C. A., Loudermilk, E. L., Miesel, J. R., O'Brien, J. J., Pausas, J. G., Hood, S., Keane, R., Morgan, P., Pingree, M. R. A., Riley, K., Safford, H., Seijo, F., Varner, J. M., Wall, T., & Watts, A. C. (2024). Principles of fire ecology. Fire Ecology, 20, 39.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.

- MacDonald, A. J., Hyon, D. W., McDaniels, A., O'Connor, K. E., Swei, A., & Briggs, C. J. (2018). Risk of vector tick exposure initially increases, then declines through time in response to wildfire in California. Ecosphere, 9, e02227.
- MacDonald, A. J., McComb, S., & Sambado, S. (2022). Linking Lyme disease ecology and epidemiology: Reservoir host identity, not richness, determines tick infection and human disease in California. Environmental Research Letters, 17, 114041.
- McLaughlin, J. P., Schroeder, J. W., White, A. M., Culhane, K., Mirts, H. E., Tarbill, G. L., Sire, L., Page, M., Baker, E. J., Moritz, M., Brashares, J., Young, H. S., & Sollmann, R. (2022). Food webs for three burn severities after wildfire in the Eldorado National Forest, California. Scientific Data, 9, 384.
- Nimmo, D. G., Andersen, A. N., Archibald, S., Boer, M. M., Brotons, L., Parr, C. L., & Tingley, M. W. (2022). Fire ecology for the 21st century: Conserving biodiversity in the age of megafire. Diversity and Distributions, 28, 350-356.
- Padgett, K. A., Casher, L. E., Stephens, S. L., & Lane, R. S. (2009). Effect of prescribed fire for tick control in California chaparral. Journal of Medical Entomology, 46, 1138-1145.
- Padgett, K. A., & Lane, R. S. (2001). Life cycle of Ixodes pacificus (Acari: Ixodidae): Timing of developmental processes under field and laboratory conditions. Journal of Medical Entomology, 38, 684-693.
- Parkins, K., York, A., & Di Stefano, J. (2018). Edge effects in fire-prone landscapes: Ecological importance and implications for fauna. Ecology and Evolution, 8, 5937-5948.
- Pascoe, E. L., Plourde, B. T., Lopéz-Perez, A. M., & Foley, J. E. (2020). Response of small mammal and tick communities to a catastrophic wildfire and implications for tick-borne pathogens. Journal of Vector Ecology, 45, 269-284.
- Pascoe, E. L., Vaughn, C. E., Jones, M. I., Barrett, R. H., Foley, J. E., & Lane, R. S. (2023). Recovery of western black-legged tick and vertebrate populations after a destructive wildfire in an intensivelystudied woodland in northern California. Journal of Vector Ecology, 48, 19-36.
- Pebesma, E., & Bivand, R. (2023). Spatial data science: With applications in R (First ed.). Chapman and Hall/CRC.
- Pellegrini, A. F. A., Hobbie, S. E., Reich, P. B., Jumpponen, A., Brookshire, E. N. J., Caprio, A. C., Coetsee, C., & Jackson, R. B. (2020). Repeated fire shifts carbon and nitrogen cycling by changing plant inputs and soil decomposition across ecosystems. Ecological Monographs, 90, e01409.
- Perry, D. A., Hessburg, P. F., Skinner, C. N., Spies, T. A., Stephens, S. L., Taylor, A. H., Franklin, J. F., McComb, B., & Riegel, G. (2011). The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management, 262, 703-717.
- R Core Team. (2024). R: A Language and Environment for Statistical Computing, Vienna, Austria: R Foundation for Statistical Computing.
- Roche, P. K., Campagne, C. S., & Ganteaume, A. (2024). Post-fire recovery dynamics and resilience of ecosystem services capacity in mediterranean-type ecosystems. Ecosystems, 27, 833-847.
- Saberi, S. J., & Harvey, B. J. (2023). What is the color when black is burned? Quantifying (re)burn severity using field and satellite remote sensing indices. Fire Ecology, 19, 24.
- Salomon, J., Hamer, S. A., & Swei, A. (2020). A beginner's guide to collecting questing hard ticks (Acari: Ixodidae): A standardized tick dragging protocol. Journal of Insect Science, 20, 11.
- Sambado, S., Dayton, G., Zilliacus, K., Dewees, S., MacDonald, A., & Briggs, C. (2025). Data from: Wildfire disturbance and ecological cascades: Teasing apart the direct and indirect effects of fire on tick populations. Dryad Digital Repository, https://doi.org/10.5061/ drvad.41ns1rnt4
- Sambado, S., MacDonald, A. J., Swei, A., & Briggs, C. J. (2024). Climateassociated variation in the within-season dynamics of juvenile ticks in California. Ecosphere, 15, e70064.

- Schoennagel, T., Balch, J. K., Brenkert-Smith, H., Dennison, P. E., Harvey, B. J., Krawchuk, M. A., Mietkiewicz, N., Morgan, P., Moritz, M. A., Rasker, R., Turner, M. G., & Whitlock, C. (2017). Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences of the United States of America, 114, 4582-4590.
- Shipley, B. (1999). Testing causal explanations in organismal biology: Causation, correlation and structural equation modelling, Oikos, 86, 374.
- Steel, Z. L., Koontz, M. J., & Safford, H. D. (2018), The changing landscape of wildfire: Burn pattern trends and implications for California's yellow pine and mixed conifer forests. Landscape Ecology, 33, 1159-1176.
- Swain, D., Abatzoglou, J. T., Albano, C., Brunner, M., Diffenbaugh, N. S., Kolden, C., Prein, A., Singh, D., Skinner, C., Swetnam, T., & Touma, D. (2025). Increasing hydroclimatic whiplash can amplify wildfire risk in a warming climate. Global Change Biology, 31, e70075.
- Swan, M., Christie, F., Sitters, H., York, A., & Di Stefano, J. (2015). Predicting faunal fire responses in heterogeneous landscapes: The role of habitat structure. Ecological Applications, 25, 2293-2305.
- Van Mantgem, E. F., Keeley, J. E., & Witter, M. (2015). Faunal responses to fire in chaparral and sage scrub in California, USA. Fire Ecology, 11. 128-148
- Wan, H. Y., Cushman, S. A., & Ganey, J. L. (2020). The effect of scale in quantifying fire impacts on species habitats. Fire Ecology, 16, 9.
- Wickham, H. (2016). ggplot2: Elegant graphics for data analysis (2nd ed.). Springer International Publishing.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. Journal of Open Source Software, 4(43), 1686.
- Wintle, B. A., Legge, S., & Woinarski, J. C. Z. (2020). After the megafires: What next for Australian wildlife? Trends in Ecology & Evolution, 35, 753-757.

#### **DATA SOURCES**

- California Department of Forestry and Fire Protection (CAL FIRE), Fire and Resources Assessment Program (FRAP) Historical Fire Perimeters [Polygon shapefile]. https://www.fire.ca.gov/what-we-do/fire-resource-assessmentprogram/fire-perimeters
- Sentinel-2 imagery (European Space Agency, 2025) was downloaded from the Copernicus Open Access Hub and processed to compute the Differenced Normalized Burn Ratio [20 m]. https://browser.dataspace.copernicus.eu
- Sentinel-2 imagery (European Space Agency, 2025) was downloaded from the Copernicus Open Access Hub and processed to compute the Normalized Differenced Normalized Vegetation Index [20 m]. https://browser.dataspace. copernicus.eu
- Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, Oregon State University. (2025a). 30-year normal temperature, 1991-2020 [~4 km]. https://prism.oregonstate.edu/normals/
- Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, Oregon State University. (2025b). 30-year normal vapor pressure deficit, 1991-2020 [~4 km], https://prism.oregonstate.edu/normals/
- Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, Oregon State University. (2025c). Daily precipitation [~4 km]. https:// prism.oregonstate.edu/normals/
- University of California Natural Reserve System (UCNRS) GIS Database Reserve Boundary Layers [Polygon shapefile]. https://ucnrs.org/research/researchresources/gis-database/

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Maps of reserves with plot locations, treatment (burned, unburned) and vegetation type. Plot coordinates were jittered by 0.001 to help with visualizations.

**Figure S2.** Tick densities with standard error by vegetation type per (A) year, and (B) reserve (shrub=shrubland, grass=grassland).

**Figure S3.** Euclidean distance (m) from plot centroid to the perimeter of fire.

Figure S4. Climate conditions by plot. 30-year normal (1991–2020) of mean annual (A) temperature (°C) and (B) vapour pressure deficit (vpd, kPA). (C) Cumulative winter precipitation (mm) calculated between December through March of each season (2021, 2022).

Figure S5. Normalized difference vegetation index (NDVI) values of burned plots per reserve and vegetation type. NDVI values were downloaded from the first week of April in 2020 (pre-fire), in 2021 (1st year spring), and in 2022 (2nd year spring). See Table S6 for exact dates. Table S1. Study design plot replicates. McLaughlin's shrubland habitat was located on Serpentine soil, which is considered unsuitable for tick populations, and was therefore excluded from this analysis. Due to extensive burning at Quail Ridge, no unburned plots were established. At Big Creek, there was insufficient unburned grasslands to sample. The Big Creek forest area was classified as Redwood forest, which can still support tick populations.

**Table S2.** Fire severity classifications were assigned to entire plot based on soil surface conditions outlined below.

Table \$3. Extended definition of plot-level measurements.

Table S4. Plot coordinates and occurrence of tick sampling. 'X' indicates whether tick sampling occurred. Vegetation types are denoted as follows: G=Grassland, O=Oak woodland, C=Chamise, R=Redwood and S=Scrub. Vegetation categories for the analysis were grassland (G), shrubland (C, S) and forest (O, R). Plot IDs follow the format: reserve-treatment-vegetation-type-replicate.

**Table S5.** Field sampling schedule. Ticks were sampled by Sambado. Plot-level vegetation measurements (Veg) were sampled by the UC Santa Cruz field team.

**Table S6.** Dates for Sentinel-2 imagery used to calculate normalized burn ratio (NBR) and normalized difference vegetation index (NDVI). Dates were acceptable when there was less than 30% cloud coverage.

Table S7. Wilcoxon signed-rank test comparing post-fire NBR to prefire NBR for paired burned plots. NBR values were downloaded from the first week of August in 2020 (pre-fire), and October 2020 (post-fire). The V statistic reflects the rank of sum of differences between post-fire and pre-fire NBR values. A V value of 0 indicates that NBR is higher (healthier vegetation) in pre-fire than post-fire. 95% confidence intervals (CI) are included with 0.05 significance level. Reserve names are McLaughlin (ML), Quail Ridge (QR), Hastings (HT) and Big Creek (BC).

**Table S8.** Summary of data sources used in the main and supplemental files with respective hyperlinks and references. For datasets with gridded spatial resolutions (i.e. 20 m or ~4 km), data were extracted at the centroid of each plot.

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