

Risk of vector tick exposure initially increases, then declines through time in response to wildfire in California

ANDREW J. MACDONALD,^{1,2,3,†} DAVID W. HYON,¹ AKIRA McDANIELS,¹
KERRY E. O'CONNOR,⁴ ANDREA SWEI,⁴ AND CHERYL J. BRIGGS¹

¹Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA

²Department of Biology, Stanford University, Stanford, California 94305 USA

³Earth Research Institute, University of California, Santa Barbara, California 93106 USA

⁴Department of Biology, San Francisco State University, San Francisco, California 94132 USA

Citation: MacDonald, A. J., D. W. Hyon, A. McDaniels, K. E. O'Connor, A. Swei, and C. J. Briggs. 2018. Risk of vector tick exposure initially increases, then declines through time in response to wildfire in California. *Ecosphere* 9(5):e02227. 10.1002/ecs2.2227

Abstract. Identifying the effects of human-driven perturbations, such as species introductions or habitat fragmentation, on the ecology and dynamics of infectious disease has become a central focus of disease ecologists. Yet, comparatively little is known about how the ecology of zoonotic disease systems responds to catastrophic disturbance events such as wildfires or hurricanes. In California, wildfire disturbance is centrally important to the ecology of forests and oak woodlands and is projected to increase in severity and extent under future climate change. Here, taking advantage of a recent wildfire as a natural experiment, we investigate the effects of wildfire disturbance on the ecology of tick-borne disease in California oak woodlands. We find that wildfire leads to elevated abundance of questing adult and nymphal western blacklegged ticks (*Ixodes pacificus*) in the year following fire, relative to unburned control plots, but that vector tick abundance declines sharply in the following two years. We find that the abundance of non-competent hosts (western fence lizards) for the Lyme disease bacterium is unaffected by fire, but that the abundances of important reproductive hosts (deer) for ticks and reservoir hosts (dusky-footed woodrats) for tick-borne pathogens are significantly negatively affected by fire. We found ticks and hosts infected with *Borrelia burgdorferi* sensu lato only within the burn extent and only in the year following the wildfire, though rates of infection were exceedingly low representing little risk to humans. In aggregate, due to the differential effects of this catastrophic disturbance event on different key host species and vector tick life stages in the transmission of tick-borne pathogens, we conclude that wildfire may potentially increase risk of exposure to vector ticks in the first year following wildfire in California, but that risk is dampened substantially in following years due to tick population declines and loss of key reservoir hosts from the system.

Key words: *Borrelia burgdorferi*; central coast California; disturbance; *Ixodes pacificus*; *Neotoma fuscipes*; *Odocoileus hemionus californicus*; *Peromyscus maniculatus*; *Sceloporus occidentalis*; wildfire.

Received 25 September 2017; revised 13 April 2018; accepted 18 April 2018. Corresponding Editor: Shannon L. LaDau.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** andy.j.macdon@gmail.com

INTRODUCTION

Understanding the role of disturbance in shaping ecological communities remains a central aim in ecology and is particularly salient in zoonotic disease systems on an increasingly altered and human-dominated planet (Bellard et al. 2012, Cardinale 2012, Kilpatrick and Randolph 2012, Lawler et al. 2014). Both human-driven and natural processes that disrupt ecological communities and ecosystem function, such as habitat fragmentation (Brownstein et al. 2005) or species invasions (Benedict et al. 2007), have been extensively studied in zoonotic and vector-borne disease systems. However, far less is understood about how the ecology of disease responds to catastrophic natural disturbance events such as hurricanes or wildfires, which could have important implications for management or public health intervention, but are challenging to anticipate.

In the fire-prone western United States, ticks transmit dozens of pathogens causing a range of diseases including Lyme disease, tick-borne relapsing fever, and anaplasmosis. Many of these disease cycles rely on transmission between tick vectors and a suite of vertebrate hosts. For example, while the causative agents of Lyme disease (*Borrelia burgdorferi* sensu stricto, s.s.), and anaplasmosis (*Anaplasma phagocytophilum*), are amplified and transmitted most efficiently by small mammal hosts such as rodents (Brown and Lane 1992, Foley et al. 2008, Salkeld et al. 2008, Swei et al. 2012), maintenance of populations of the primary vector, *Ixodes pacificus*, is tied to large, wide-ranging mammals such as mule deer (*Odocoileus hemionus*) that act as reproductive hosts for adult ticks (Lane and Burgdorfer 1986). Further, host preference is specific to tick life stage: Larval and nymphal ticks feed primarily on small vertebrate hosts, while adult ticks seek large mammal hosts from understory vegetation (Eisen et al. 2001, 2003, Casher et al. 2002, Lane et al. 2009, MacDonald and Briggs 2016). Thus, the effects of perturbations on the ecology of tick-borne disease systems will strongly depend on how each group of hosts and each tick life stage responds to the disturbance (Swei et al. 2012). This response will largely be determined by the variable habitat requirements and spatial ranges of key host species, and the degree to

which the disturbance alters important host and vector tick habitat.

In the western United States, wildfire is one of the most important and significant natural, as well as anthropogenic, disturbances and plays a central role in the ecology of Californian forests (Steel et al. 2015). While California oak woodlands were burned regularly by Native Americans as part of early land management practices (Stephens et al. 2007, Collins et al. 2017), comparatively recent changes in forestry practices, including fire suppression and fuels management, have contributed to an increase in the number and severity of wildfires in the state. Further, in California, wildfire activity has increased in recent years and is expected to increase into the future due to climate change (Westerling and Bryant 2007, Westerling et al. 2011, Westerling 2016). Wildfires have pervasive effects on entire communities from direct effects of mortality associated with fire itself (Smith et al. 2012) to post-fire succession and associated effects on herbivores and their predators (Swanson et al. 2011). These effects may have implications for tick populations, potentially directly from mortality during wildfire events, as well as indirectly through changes in environmental conditions resulting from loss of vegetation or through effects on vertebrate hosts (Lawrence 1966, Alverson et al. 1988, Allan 2009). Given the widespread distribution, frequency, and proximity of wildfire disturbance to human population centers in California (Fig. 1), and expectations that wildfire frequency and intensity are likely to increase under climate change (Westerling and Bryant 2007, Westerling et al. 2011, Westerling 2016), better understanding of the impacts of fire on ticks and their hosts will be critical to predicting changing patterns of disease risk associated with tick-borne pathogens in California.

While investigating the effects of fire on tick abundance and tick-borne disease risk has been of interest to disease ecologists and public health practitioners in its possible application as an intervention measure for the prevention of human disease (Stafford et al. 1998, Padgett et al. 2009), these effects have been explored only utilizing controlled burns. Further, these studies have tended to focus only on the effects of fire on questing tick abundance (Hoch et al. 1972, Scifres et al. 1988, Spickett et al. 1992, Davidson

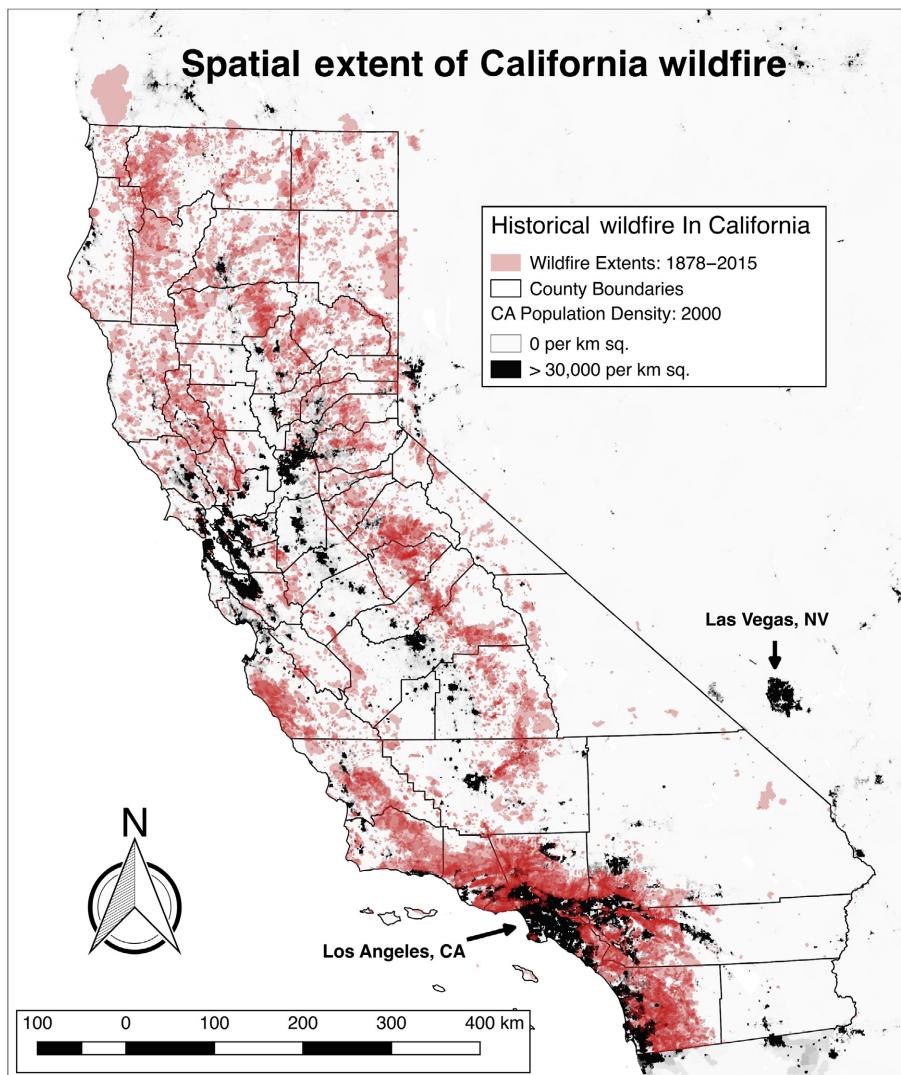


Fig. 1. Map of historical wildfire extents in California, USA, and human population centers in the state; darker red indicates higher burn frequency (e.g., in wildlands surrounding Los Angeles in southern California), and darker gray indicates higher population density (people/km²). Fire perimeter data are from Cal Fire (http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download), and United Nations adjusted human population density data for the year 2000 are from the NASA Socioeconomic Data and Applications Center (<http://sedac.ciesin.columbia.edu/data/collection/gpw-v4>).

et al. 1994, Stafford et al. 1998, Horak et al. 2006), with only limited attention paid to concurrent effects on key species of tick (or blood meal) hosts (Allan 2009, e.g., Padgett et al. 2009). This limits inference about the ecological mechanisms producing observed patterns of tick abundance, as well as about the potential long-term implications of fire disturbance for the ecology of

tick-borne pathogens and possible changes in human disease risk.

Studies of controlled burns have found mixed results of the effects of fire on tick populations and disease risk, depending on the tick species (Spickett et al. 1992, Horak et al. 2006), the severity of the fire (Stafford et al. 1998), the frequency of prescribed burns (Davidson et al.

1994, Cully 1999), and patterns of seasonal activity or host preferences of vector ticks (Spickett et al. 1992, Horak et al. 2006). For example, in southern Africa, Horak and colleagues (2006) find no effect of fire on abundance of the tick *Amblyomma hebraeum*, which feeds primarily on large, wide-ranging herbivorous mammal hosts that are often attracted to new growth following fire for forage (Horak et al. 2006). However, in the same study, other species of tick with life stages that feed primarily on small mammal and rodent hosts (e.g., *Dermacentor rhinocerinus* and *Rhipicephalus simus*), which can experience local population declines following fire due to reduced cover and food availability, were found to decrease significantly in abundance following fire (Horak et al. 2006). Burn frequency has also been found to be associated with tick abundance; for example, annual fires have been shown to depress populations of the lone star tick (*Amblyomma americanum*) in the southeast and great plains regions of the United States (Davidson et al. 1994, Cully 1999). Similarly, higher severity prescribed burns have also been found to lead to larger reductions than low-severity prescribed burns in populations of *Ixodes scapularis*, the primary vector of *B. burgdorferi* s.s. in eastern North America (Stafford et al. 1998), though these effects were limited to the year of the burn. Long-term prescribed burning regimes, on the other hand, have been found to consistently reduce tick populations, including *I. scapularis*, in the southeastern United States (Gleim et al. 2014). Finally, one of the only studies of the effect of prescribed fire on *I. pacificus*, the primary (and hypothesized) vector of numerous pathogens including *B. burgdorferi* s.s., *Borrelia miyamotoi*, *A. phagocytophilum*, and *Babesia odocoilei* (Eshoo et al. 2015) in the fire-prone western United States, found no difference in questing adult tick abundance between burned and unburned control plots in the year following prescribed fire (Padgett et al. 2009). Moreover, the same study found no difference or significantly higher rates of juvenile tick infestation of rodent hosts, depending on the controlled burn, in burned as compared with unburned control plots (Padgett et al. 2009).

Prescribed fires, however, tend to be relatively small in geographic area and low in intensity

and severity. Unlike prescribed fires, wildfires can burn very large areas of forest and other habitat, and have the potential to burn at higher temperatures leading to more destruction of leaf litter, duff, and belowground organic material (Neary et al. 1999). Wildfires thus have the potential to have greater effects on tick abundance, potentially directly through mortality as well as indirectly through effects on vertebrate host abundance and abiotic and habitat conditions, than do prescribed burns. Yet, given the unpredictability of wildfires, and the substantial challenges associated with studying wildfire in an experimental context, their effect on vector ticks and the community of key hosts in the transmission of tick-borne pathogens have not been explored. Here, we report the results of the first investigation, to our knowledge, of the effect of wildfire on both vector tick and vertebrate host abundance in California using a recent wildfire in the central coast region of the state as a natural experiment. We sampled tick populations and vertebrate host communities within and adjacent to the burn extent for three years following the fire to track the response of each parasitic life stage of the vector, and key vertebrate host species, to wildfire disturbance.

METHODS

Field sampling was conducted in the Los Padres National Forest (NF) of Santa Barbara County, California (34°33'06.22" N, 119°46'43.15" W). This region is characterized by a Mediterranean climate with relatively cool, wet winters and warm, dry summers. With the onset of the summer dry season in California comes elevated wildfire risk, when live fuel moisture declines, increasing the chance of ignition (Roberts et al. 2006). This study took advantage of the May 2013 White Fire as a natural experiment, which burned ~800 ha of oak woodland and oak savannah habitat in Los Padres NF while leaving neighboring oak woodland habitat unaffected (Fig. 2). The fire began 27 May 2013 and more than doubled in size from ~280 to ~730 ha on 28 May as high winds fanned the flames. Throughout much of the burn area, scorch height was well into the oak canopy and all aboveground vegetation was removed by the fire, with the exception of scorched woody stems and large oak trees, with surface soil reduced to gravel leading

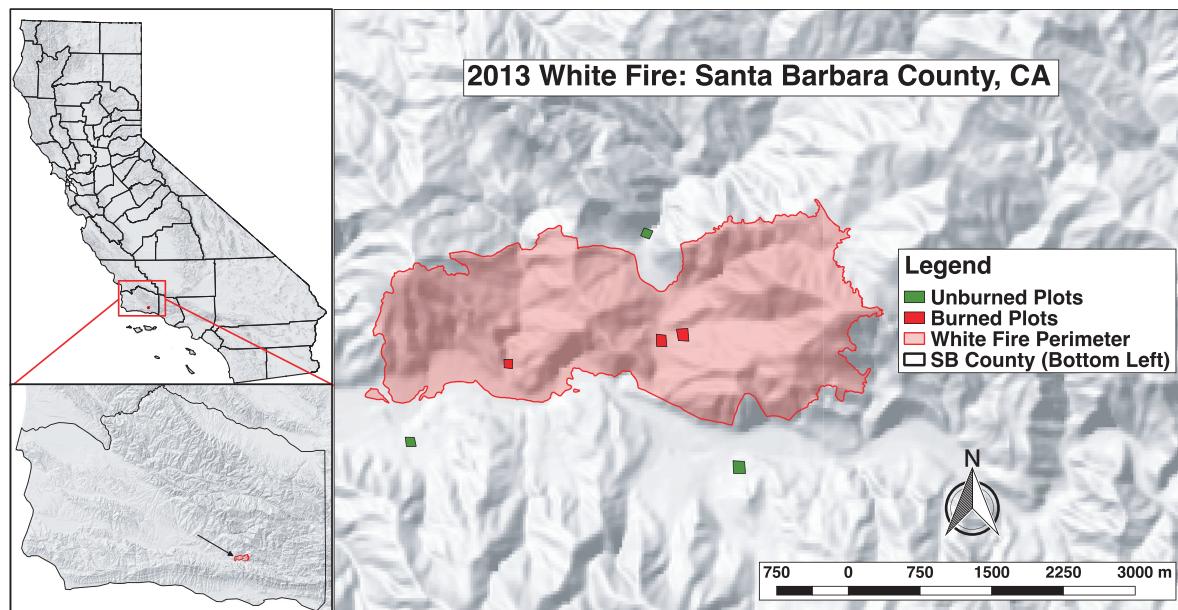


Fig. 2. Map of study area, including six 1-ha plots within and adjacent to the perimeter of the White Fire (May 2013), Santa Barbara County, California, USA. White Fire perimeter data layer was obtained from Cal Fire (http://frap.cdf.ca.gov/data/frapgisdata-sw-fireperimeters_download), and the California hillshade data layer was obtained from Cal-Atlas (www.atlas.ca.gov/download.html) through <https://koordinates.com>.

to slope erosion within the burn perimeter (Fig. 3). The White Fire was larger than the average historical wildfire in California, and over six times the size of the average prescribed burn in the state, based on historical fire perimeter data from Cal Fire (Fig. 1). Given the size and vegetation impacts of the fire (Fig. 4), the severity of the burn was considerably higher than the typical prescribed burn. Within the Los Padres NF, six 1-ha sites were chosen, three in oak woodland habitat within the fire perimeter and three in oak woodland habitat adjacent to the burn to sample abundance of ticks and hosts. These six sites were located within a ~4-km² area and were chosen to minimize variation in background (pre-fire) microclimate or habitat differences between sites. We selected only dense oak woodland sites because this habitat type has been found to be associated with elevated densities of *Ixodes pacificus* (Eisen et al. 2003, 2006, Swei et al. 2011a), the primary vector of numerous tick-borne pathogens in the western United States.

Site-specific habitat, abiotic, and environmental data relevant to tick and host populations were

collected each year of the study (2013–2016), and the variables were chosen based on previous studies (Padgett and Lane 2001, Eisen et al. 2003, Swei et al. 2011a, MacDonald et al. 2017), in order to track environmental conditions and recovery of vegetation following the fire. Data loggers, placed in each site just above ground level and protected from direct solar radiation, collected hourly temperature data (iButtons, Maxim Integrated, San Jose, California, USA). From the data loggers, we calculated average maximum and minimum daily temperature over the dry (1 May–31 October) and rainy (1 November–30 April) seasons. We also measured overstory canopy cover, stem density (number of stems >5 cm in diameter at breast height and >1.5 m in height), slope and elevation, percent cover of dense leaf litter (>5 cm in depth), grass/herbaceous vegetation, understory woody vegetation (e.g., *Artemisia californica*, *Toxicodendron diversilobum*), and bare-ground microhabitats in each site. These variables were included in models of the effect of wildfire on tick and host abundance (see *Statistical analyses*) to control for factors, other

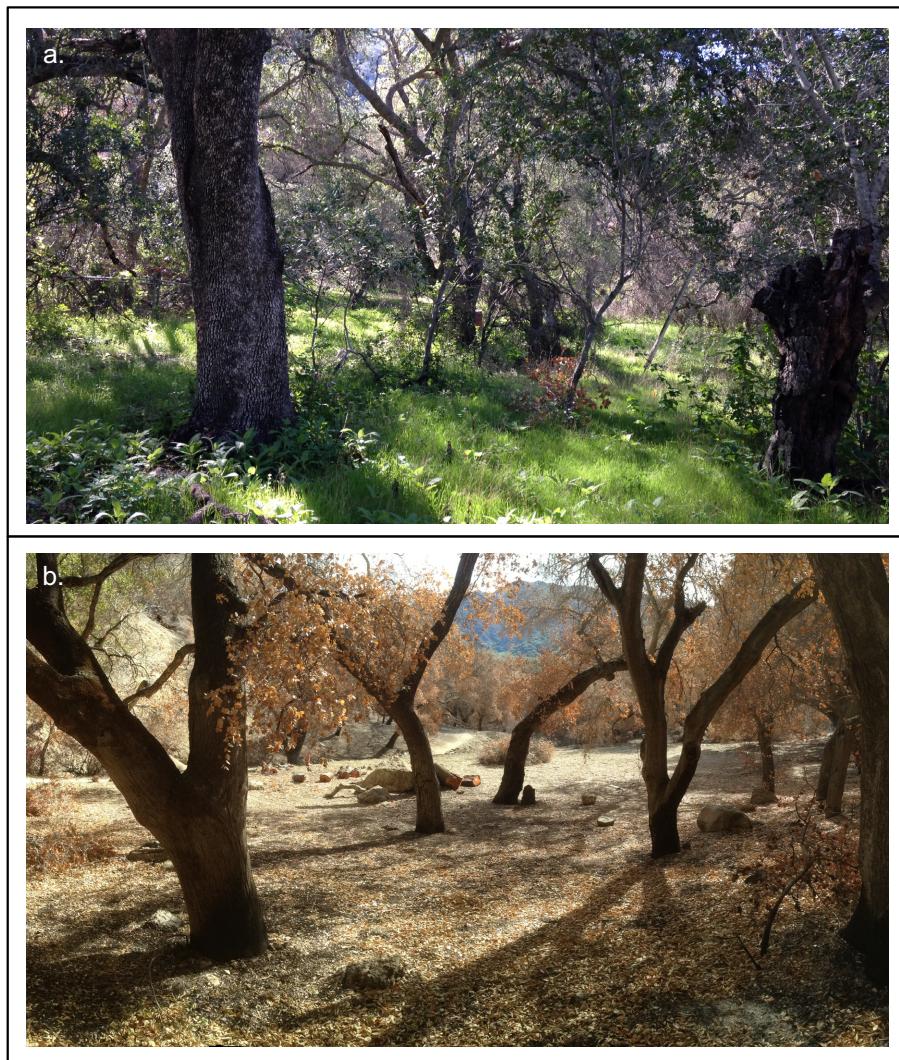


Fig. 3. Photographs of representative study plots that were (a) unburned and (b) burned. The fire removed understory vegetation and accumulated debris (e.g., dead logs and downed branches), and removed surface soil organic matter leading to erosion, and scorch height was well into the canopy (b). Photographs were taken in the winter of 2014, when sampling first began in the year following the fire.

than wildfire, that have previously been shown to influence tick and host populations (Padgett and Lane 2001, Eisen et al. 2003, Swei et al. 2011a).

Tick and vertebrate host sampling

Ticks were sampled within each of the 1-ha sites approximately monthly between early February and early June of 2014–2015, and between early March and early May of 2016, encompassing periods of peak seasonal activity of all three parasitic life stages in this region

(MacDonald and Briggs 2016). A total area of 4000 m² was sampled at each site in 2014 and 2015 and 2000 m² each in 2016. Sampling in 2016 was interrupted by periodic flooding of roads and debris flows, which limited access to the field sites throughout the season, so a smaller total area was sampled in 2016 than in 2014–2015. Ticks were collected using the drag method in which a 1-m² white flannel cloth is dragged along the ground and understory vegetation and periodically checked for attached ticks. In total,

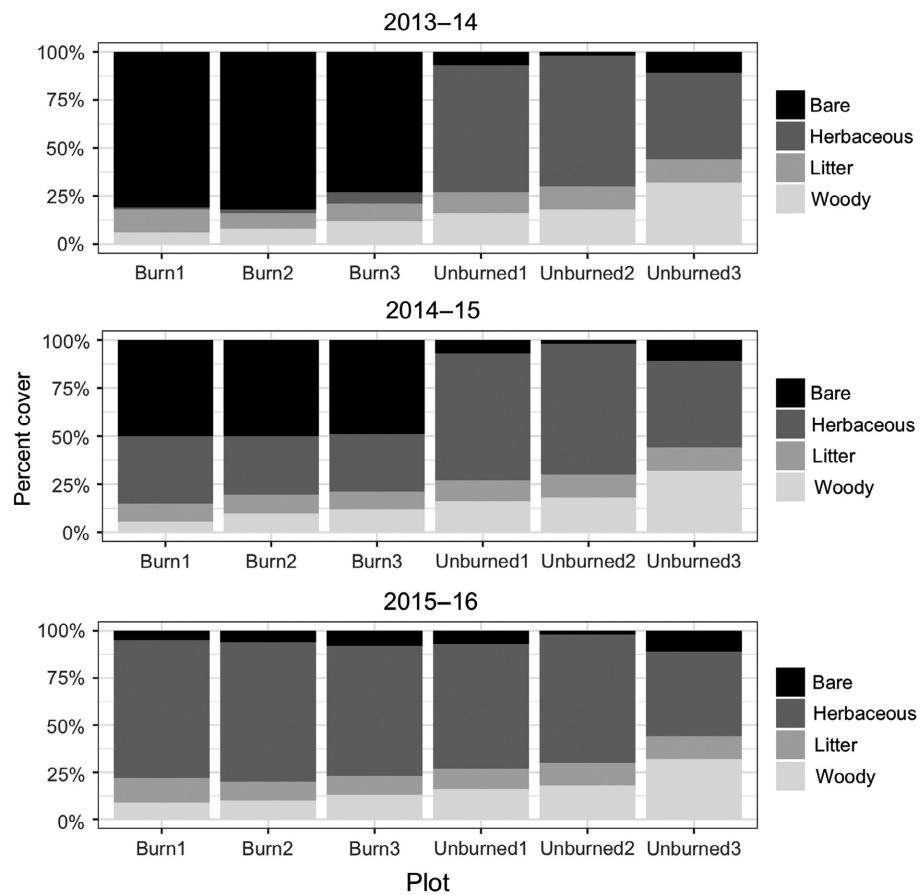


Fig. 4. Percent vegetation cover of each sampled plot through time to illustrate the effects of fire on tick and host habitat. Burned plots recovered to conditions that approximated observed conditions in adjacent unburned plots by the third year of the study, over three years post-fire. Data were collected in April of each year, in the middle of the rainy season.

50 separate 10-m transects were sampled in each site, each collection date, and the flannel cloth checked for attached ticks after each transect. These transects were revisited and resampled eight times in 2014–2015, and four times in 2016. Ticks were stored in 70% EtOH for later identification, using a dichotomous key for the ticks of California, and pathogen testing by polymerase chain reaction (PCR).

Small mammals such as dusky-footed woodrats (*Neotoma fuscipes*) and western gray squirrels (*Sciurus griseus*) are important reservoir hosts for tick-borne pathogens in California, including *Borrelia burgdorferi* s.s. and *Anaplasma phagocytophilum*, while other common species such as deer mice (*Peromyscus maniculatus*) can act as reservoirs, even though they are less

competent (Lane and Brown 1991, Brown and Lane 1992, Lane et al. 2005, Foley et al. 2008, Salkeld et al. 2008, Salkeld and Lane 2010, Sweig et al. 2012). A 10 × 10 trapping grid was established at each of the six sites to estimate relative abundance of small mammal hosts. Each trap station was located 10 m apart from adjacent trap stations and included two extra-large Sherman live traps (7.6 × 9.5 × 30.5 cm; H.B. Sherman Traps, Tallahassee, Florida, USA), for a total of 200 traps per grid. Mark–recapture trapping took place for three consecutive nights at each site between mid-March and mid-May 2014. Captured mammals were anesthetized to collect ear tissue samples using sterile biopsy punches (Integra Miltex, York, Pennsylvania, USA) and ectoparasites and tagged with an individually

numbered eartag (National Band & Tag Company, Newport, Kentucky, USA) for identification of recaptured animals.

Western fence lizards (*Sceloporus occidentalis*) are important hosts for immature *I. pacificus* (Casher et al. 2002). They are also non-competent hosts for *B. burgdorferi* s.s. in California, because they cleanse ticks of infection with the pathogen (Lane and Quistad 1998). *Sceloporus occidentalis* abundance was estimated using a “sight–re-sight” protocol in which five of the ten transects of each of the six trapping grids were surveyed for *S. occidentalis* between mid-March and mid-May, 2014. *Sceloporus occidentalis* were marked with a diluted latex paint mixture using a tree-marking gun (Swei et al. 2011b). Three different colors of paint were used, one for each of three consecutive days to determine encounter history (Swei et al. 2011b). *Sceloporus occidentalis* were also captured using nooses at each of the six sites between early March and early May 2014 in order to estimate tick burdens.

Because small vertebrate host sampling was undertaken in only the first year following the fire (2014), density of inhabited *N. fuscipes* middens (Hamm et al. 2002) was also surveyed each year as a proxy for small vertebrate host abundance to include as a covariate in models of tick abundance (see *Statistical analyses*). Density of inhabited *N. fuscipes* middens was used because it has been found to be a good proxy for small vertebrate host abundance both in this study (Spearman’s correlation coefficient between sampled small vertebrate host abundance and density of inhabited woodrat middens, $\rho = 0.64$) and in previous studies (Bolger et al. 1997, Tietje et al. 1997). In addition, *N. fuscipes* is an important reservoir for tick-borne pathogens in California, and a previous study found that controlled burns in northern California removed *N. fuscipes* from the system for at least one year following the burn (Padgett et al. 2009).

Finally, deer are important reproductive hosts for adult *I. pacificus* (Lane and Burgdorfer 1986). California mule deer (*Odocoileus hemionus californicus*) use of each site was estimated using standardized pellet-group counts in which five, 4 × 22 m, randomly assigned subplots within each site were surveyed for pellet groups (>4 pellets/group) and subsequently cleared. Each of these subplots was then re-surveyed and new

pellet groups quantified (White and Eberhardt 1980, Rowland et al. 1984) in the fall and spring of each year of the study. Pellet-group data were summed across all subplots within a site to obtain relative measures of *O. h. californicus* use.

Infection with *Borrelia burgdorferi* sensu lato

Lyme disease is the most common tick-borne disease in human populations in the western United States, so collected samples were assayed for infection with *B. burgdorferi* sensu lato (s.l.) group spirochetes. DNA was extracted from collected ticks and small mammal tissue samples using a Qiagen DNeasy extraction kit (Qiagen, Valencia, California, USA) following the manufacturer’s instructions. All samples were then screened for infection with *B. burgdorferi* s.l. via nested PCR targeting the 5S–23S rRNA spacer region of all borreliae belonging to this group, which includes *B. burgdorferi* s.s., following the methods outlined in Lane et al. (2004). Polymerase chain reaction-positive samples were sequenced at the 5S–23S intergenic spacer region following Lane et al. (2004), and sequenced on an AB 3100 (Applied Biosystems, Foster City, California, USA).

Statistical analyses

Generalized linear mixed-effects models (GLMMs) were used to determine the effect of wildfire on abundance of *I. pacificus* of each life stage. Because this study took advantage of a natural experiment, which by definition precludes random assignment of treatment and control, additional factors known to influence tick abundance were included in models to control for their effects on tick abundance and to reduce bias in the estimation of the effect of wildfire. Counts of *I. pacificus* per collection date per site were the outcome variables, regressed against whether the site was burned or not, year of the study (2014–2016, 1 yr post-fire to 3 yr post-fire), Julian day² (to account for seasonal effects), site-specific habitat characteristics, maximum average wet- and dry-season temperature, and density of inhabited *N. fuscipes* middens (a proxy for small vertebrate host abundance), all included as fixed effects. Site was included as a random effect to control for repeated measures in each site sampled. An interaction term between burn status and year was included to determine whether the

effect of being burned changed from year to year as the system recovered following the fire. In addition, lagged relative *O. h. californicus* activity was included in the model predicting larval tick abundance. Adult female *I. pacificus* ticks lay eggs in the spring at the site where they drop off of *O. h. californicus*, or other large vertebrate hosts, following blood meals; these eggs hatch into larval ticks in the summer and emerge to seek hosts the following spring (Padgett and Lane 2001). Thus, *O. h. californicus* activity in the previous spring would be expected to predict larval tick abundance in the current year. In contrast, nymphal and adult tick abundance would be expected to respond more directly to small vertebrate host abundance in the previous year, due to the host preferences of larval and nymphal ticks, while *O. h. californicus* activity would not be expected to be predictive of nymphal and adult tick abundance, so was not included in these models. The full model of tick abundance for each life stage included each of these fixed and random effects described above. Model selection was based on Akaike weights derived from AIC_c and WAIC.

The effect of wildfire on key hosts in the transmission of *B. burgdorferi* s.s. (e.g., *N. fuscipes*) as well as key hosts in the maintenance of tick populations (e.g., *O. h. californicus* and *S. occidentalis*) was also of interest, in order to understand and predict potential longer-term impacts of wildfire on risk of tick exposure and tick-borne disease ecology. Thus, GLMMs were also used independently to determine the effect of wildfire on relative activity of *O. h. californicus*. The measure of relative *O. h. californicus* activity was regressed against the same set of fixed and random covariates as the models of tick abundance, with the exception of *N. fuscipes* density, and candidate models chosen using identical model selection criteria as above. Generalized linear mixed-effects models with Poisson error distributions for count data were implemented using the package "lme4" (Bates et al. 2015) in R (R Core Team 2016) for adult *I. pacificus* and *O. h. californicus* activity, because they produced the best fit to the data. Generalized linear mixed-effects models with zero-inflated negative binomial error distributions were implemented using the package "pscl" (Zeileis et al. 2008) in R (R Core Team 2016) for nymphal and larval *I. pacificus*

abundance, due to overdispersion in the data as well as the relatively low probability of encountering these life stages in southern as compared to northern California (MacDonald and Briggs 2016), resulting in excess zeros in the data.

In order to estimate relative abundance of small vertebrate hosts in the year following the fire (2014) within and adjacent to the fire perimeter, a Huggins closed population mark–recapture model was used (Huggins 1989). Each common species (*P. maniculatus*, *N. fuscipes*, and *S. occidentalis*) was analyzed individually by site, for each of the six sampling sites using the "mra" package (McDonald 2015) in R (R Core Team 2016). Population estimates for small vertebrate hosts were produced only for the year following the fire (2014), because host sampling was conducted only in this year. A partial least squares regression (PLSR) approach (Carrascal et al. 2009) was utilized to determine the effect of wildfire, and other covariates, on populations of important host species in the year following the fire. Separate PLSR models were specified for each small vertebrate host species to determine whether wildfire had a significant effect on relative abundance. Partial least squares regression models were similarly used to determine whether wildfire had a significant impact on average tick burdens for each species of small vertebrate host. Partial least squares regression models were run in R (R Core Team 2016) using the package "plsdepot" (Sanchez 2012).

RESULTS

Wildfire had a clear effect on tick and host habitat and vegetation cover in the study area, with burned plots dominated by bare-ground microhabitats in the winter and spring immediately following the fire, recovering to comparable vegetation cover to unburned control plots by the final year of the study, three years post-fire (Fig. 4). This loss of vegetation and organic material also appeared to have an effect on microclimates in the first year of the study. While maximum average winter temperature was not significantly higher in burned sites in the year following the fire, 2013–2014 (two-sample *t* test comparing burned and unburned mean temperatures: *t*(202.46) = 1.0835, *P* = 0.14), maximum average summer temperature in the following summer—2014—was significantly

higher in burned sites ($t(365.98) = 4.1517$, $P < 0.0001$). These differences in microclimatic conditions between burned and unburned sites were no longer present in the second and third years of the study.

Tick communities sampled in this region were dominated by western blacklegged ticks (*Ixodes pacificus*), which made up ~94.4% of all 557 ticks collected, across all life stages. Pacific coast ticks (*Dermacentor occidentalis*) were also encountered, making up the other ~5.6% (Fig. 5; Appendix S1: Table S1). Tick abundance is likely to be influenced by other factors beyond burn status, such as temperature or habitat conditions. Using GLMMs to control for these potentially confounding factors reveals a significant positive effect of wildfire on adult tick abundance (Table 1). However, the interaction between year and wildfire reveals a significant negative effect in the second and third years post-fire (Table 1), which is visually evident in the raw data illustrating annual patterns of abundance (Fig. 5; Appendix S1: Table S1). Nymphal *I. pacificus* display a similar pattern, but with abundance declining to zero within the fire perimeter in the second and third years post-fire (Fig. 5; Appendix S1: Table S1). Again, statistical model results indicate a significant positive effect of wildfire on nymphal tick abundance, but no significant interaction between burn status and year (Table 1), despite the absence of nymphal ticks from burned sites in 2015 and 2016. Larval *I. pacificus*, on the other hand, were more immediately negatively affected with significantly reduced abundance within the fire perimeter in the first year, and declining to zero in years 2 and 3 post-fire (Fig. 5, Table 1; Appendix S1: Table S1).

Deer herds in the Los Padres NF of Santa Barbara County are comprised primarily of California mule deer (*O. h. californicus*). Relative abundance of *O. h. californicus* in the year following the fire was substantially lower within the fire perimeter than in adjacent sites, though rebounded in subsequent years (Fig. 6). Model results indicate a significant negative effect of wildfire on abundance of deer (Table 1). However, the interaction of burn status with year indicates that deer activity was less negatively impacted in the second year post-fire, and was comparable to unburned control plots by the third year of the study (Table 1, Fig. 6).

Small vertebrate host communities were dominated by western fence lizards (*S. occidentalis*), deer mice (*Peromyscus maniculatus*), and dusky-footed woodrats (*Neotoma fuscipes*), though southern alligator lizards (*Elgaria multicarinata*), Merriam's chipmunks (*Tamias merriami*), and California ground squirrels (*Otospermophilus beecheyi*) were also captured in this study (Appendix S1: Table S2). In the first year following the fire, abundance of *P. maniculatus* was indistinguishable between burned and unburned sites (Fig. 6), and PLSR model results indicate no significant effect of wildfire on observed patterns of abundance (Table 2; Appendix S1: Table S3). Similarly, abundance of *S. occidentalis* was not affected by wildfire (Fig. 6, Table 2; Appendix S1: Table S3). However, wildfire did have a significant negative effect on the abundance of *N. fuscipes*, as observed in earlier studies of prescribed burns (Padgett et al. 2009), with population estimates reduced to zero within the fire perimeter (Fig. 6, Table 2; Appendix S1: Table S3). Further, *N. fuscipes* middens were destroyed in the fire, with limited evidence for construction of new middens or post-fire recolonization until the third and final year of the study (Appendix S1: Fig. S1). Recolonization and construction of new nests within the burn extent represented only a small fraction of all inhabited nests across all study sites (~5%).

The distribution of tick burdens or number of attached ticks per host largely followed this same pattern of host abundance, with no detectable effect of wildfire on *P. maniculatus* tick burdens. There was a small positive effect of wildfire on the residual variation in *S. occidentalis* tick burdens (Table 2; Appendix S1: Table S4), though this effect was only observed acting on the small amount of variation unexplained by the first component and thus contributed minimally to general patterns of tick burdens. Overall, tick burdens were slightly lower in sites impacted by wildfire on both *P. maniculatus* and *S. occidentalis* (Fig. 6). Further, because *N. fuscipes* were not captured in sites impacted by wildfire, no body burdens of blacklegged ticks were detected on this species within the fire perimeter (Fig. 6, Table 2; Appendix S1: Table S4). The reduced *O. h. californicus* activity as well as lower tick burdens on small vertebrate hosts and loss of *N. fuscipes* observed in sites impacted by wildfire may explain the elevated abundance of questing adult

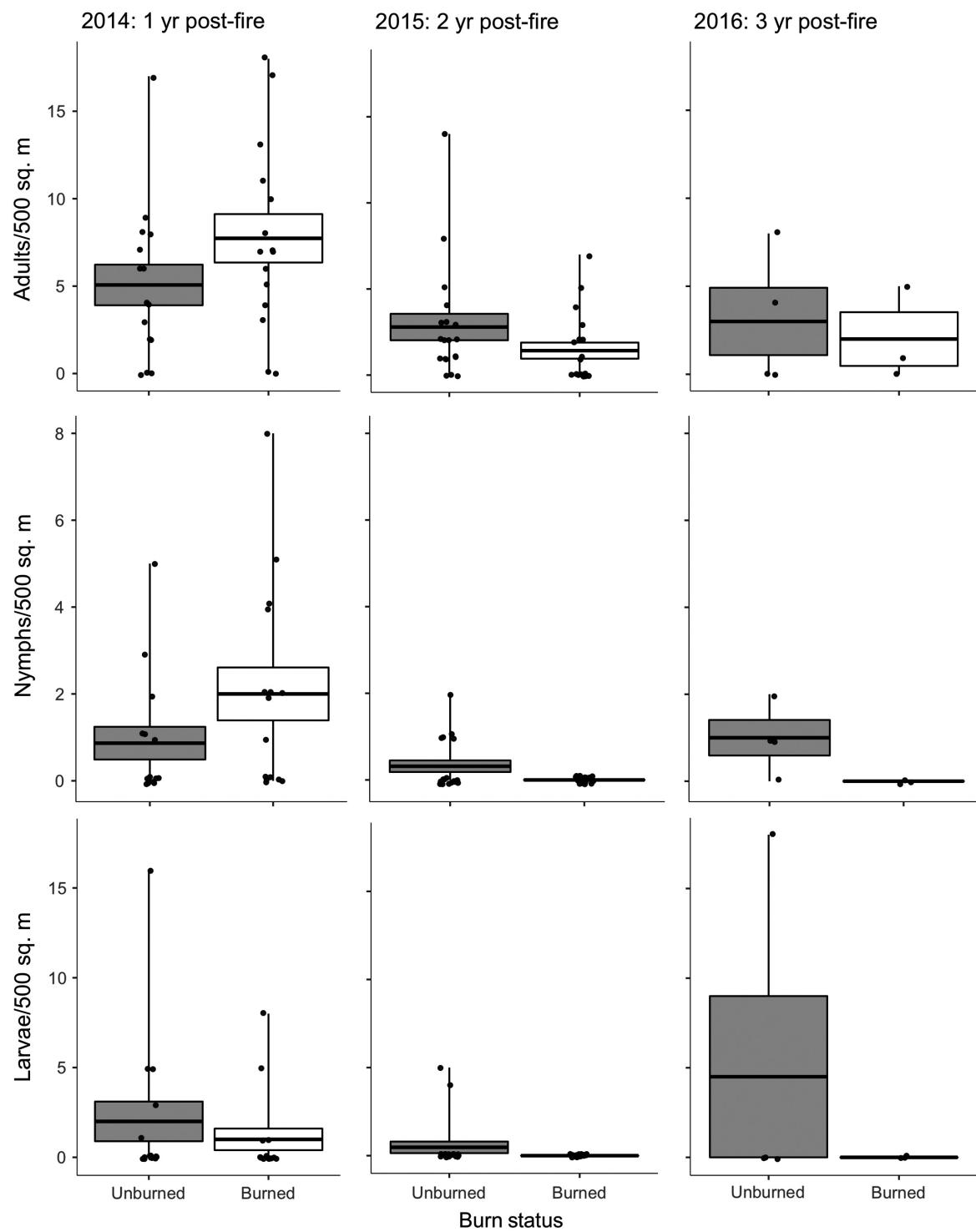


Fig. 5. Adult (a), nymphal (b), and larval (c) *Ixodes pacificus* abundance (no./500 m²) by year, by burn status (gray, "Unburned"; white, "Burned"). Boxplots with standard errors and individual sample points represent a summary of the raw collection data. Statistical analysis of the effect of wildfire on tick abundance by life stage, controlling for other factors that could be influencing patterns of abundance, is presented in Table 1.

Table 1. Generalized linear mixed-effects model results for *Ixodes pacificus* abundance by stage, and deer (*Odocoileus hemionus californicus*) activity for the 2013–2014 through 2015–2016 seasons (1–3 yr post-fire).

Variable	Adult <i>I. pacificus</i>		Nymphal <i>I. pacificus</i>		Larval <i>I. pacificus</i>		<i>O. hemionus californicus</i>	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	0.49	0.047*	-2.07	0.004**	8.11	<0.001***	3.12	<0.001***
Burned	2.57	<0.001***	4.87	<0.001***	-18.15	0.001**	-1.62	<0.001***
Year: 2015	-0.81	<0.001***	-0.82	0.114	-2.03	0.004**	0.38	<0.001***
Year: 2016	-0.11	0.72	0.08	0.889	-0.42	0.599	0.38	<0.001***
Julian Day ²	-0.50	<0.001***	0.53	0.006**	-0.46	0.042*	NA	NA
Maximum summer temperature	NA	NA	-1.70	<0.001***	NA	NA	NA	NA
Maximum winter temperature	NA	NA	NA	NA	-1.29	0.003**	NA	NA
Bare-ground cover	NA	NA	NA	NA	7.42	0.002**	NA	NA
Canopy cover	NA	NA	NA	NA	NA	NA	0.15	<0.001***
Woodrat nest density	1.08	<0.001***	NA	NA	NA	NA	NA	NA
Burned × year: 2015	-1.10	<0.001***	-0.20	0.996	-9.19	0.994	0.96	<0.001***
Burned × year: 2016	-1.12	0.03	-0.24	0.998	5.15	0.995	1.75	<0.001***

Notes: Generalized linear mixed-effects model results for adult (Poisson, log link), nymphal (negative binomial, log link), and larval (negative binomial, log link) *I. pacificus* abundance, and *O. hemionus californicus* (Poisson, log link) plot use. Results are shown as model estimates and P values. Levels of significance are as follows: *P ≤ 0.05, **P ≤ 0.01, and ***P ≤ 0.001. Values in boldface indicate significant effects of wildfire on tick abundance and deer activity.

and nymphal *I. pacificus*, respectively, in the year immediately following wildfire in this study.

A total of 296 adult and 53 nymphal *I. pacificus* ticks, as well as 72 *P. maniculatus* and 31 *N. fuscipes*, were assayed for infection with *Borrelia burgdorferi* s.l. While infection prevalence was extremely low, as in previous studies conducted in southern California (Lane et al. 2013, Padgett et al. 2014, Billeter et al. 2017, MacDonald et al. 2017), infected hosts were only identified from within the burn extent (two *P. maniculatus* infected with *Borrelia bissetiae*; Appendix S1: Table S5) and infected ticks were only identified from within the burn extent in the year following the fire (two nymphs, one infected with *Borrelia californiensis* and one with *B. burgdorferi* s.l. CA393; Appendix S1: Table S4). No ticks or hosts were infected with the causative agent of Lyme disease, *B. burgdorferi* s.s. in this study, though infection has been detected in the broader region (MacDonald et al. 2017).

DISCUSSION

Wildfire is one of the most significant and important natural disturbances in the western United States, with impacts on everything from patterns of biodiversity to nutrient cycling and carbon storage (North and Hurteau 2011, Steel et al. 2015). Moreover, wildfire frequency and

extent are expected to increase in California into the future under projected climate change, with impacts on forested habitats increasing statewide (Westerling and Bryant 2007, Westerling et al. 2011, Westerling 2016). These same habitats support the tick and host populations necessary for maintenance and transmission of numerous tick-borne pathogens. Using the Santa Barbara County White Fire as a natural experiment, our study found that, in contrast to expectations, wildfire initially leads to elevated abundance of questing ticks on the landscape and therefore potential tick exposure, with subsequent dampening of risk through time. This provides some of the first evidence suggesting that wildfire disturbance may have different consequences for the ecology of tick-borne disease systems than do prescribed burns in the western United States. Specifically, our study investigated the effect of wildfire on important host species and populations of *Ixodes pacificus*, the primary vector of the causative agents of Lyme disease, tick-borne relapsing fever, and anaplasmosis in the western United States, for three years following the White Fire to determine the potential aggregate effect on tick-borne disease ecology and risk of tick exposure.

Notably, the abundance of both questing adult and nymphal *I. pacificus* was elevated in the year following the wildfire. Because this fire occurred during the last week of May of 2013, at the very

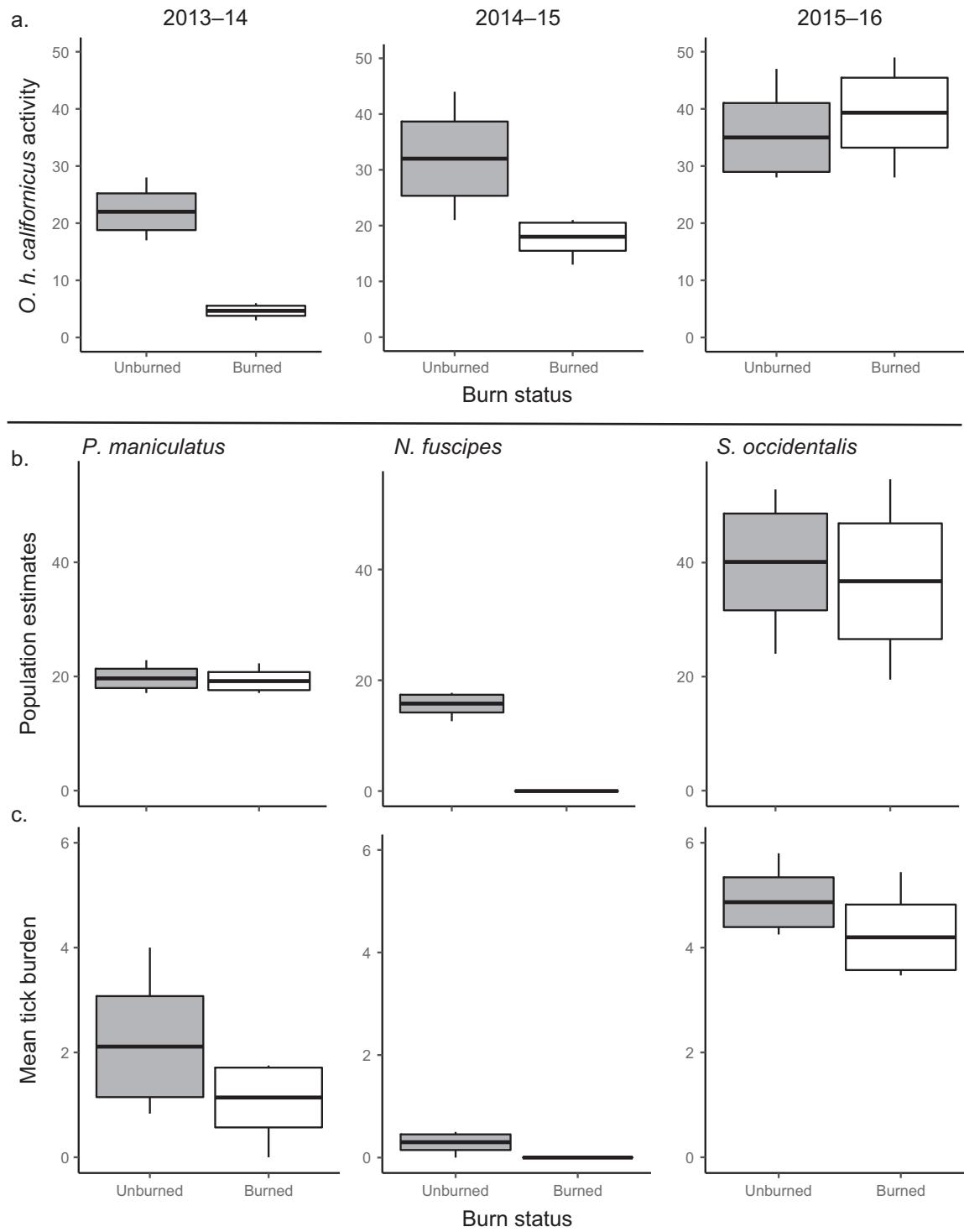


Fig. 6. Deer (*Odocoileus hemionus californicus*) plot use by year (2013–2016), by burn status (a); small vertebrate host (*Peromyscus maniculatus*, *Neotoma fuscipes*, and *Sceloporus occidentalis*) population estimates (b), and immature *Ixodes pacificus* tick burdens (c) in 2014 (1 yr post-fire), by burn status (gray, “Unburned”; white, “Burned”). Data represented as boxplots with standard errors.

Table 2. Partial least squares regression results for small vertebrate host abundance and tick burdens in 2014 (1 yr post-fire).

Model outcomes	<i>Peromyscus maniculatus</i>					<i>Neotoma fuscipes</i>					<i>Sceloporus occidentalis</i>				
	Comp 1 wts	VIP	Comp 2 wts	VIP	Full model	Comp 1 wts	VIP	Comp 2 wts	VIP	Full model	Comp 1 wts	VIP	Comp 2 wts	VIP	Full model
Effect of fire on host populations	-0.11	0.36	0.05	0.17	-	-0.39	1.23	0.11	0.34	-	-0.09	0.28	0.31	0.98	-
R ²	0.73	-	0.18	-	-	0.88	-	0.08	-	-	0.89	-	0.04	-	-
Cum. R ²	-	-	-	-	0.91	-	-	-	-	0.96	-	-	-	-	0.93
Effect of fire on host tick burdens	-0.30	0.95	0.29	0.93	-	-0.39	1.24	0.11	0.34	-	-0.25	0.78	0.34	1.09	-
R ²	0.36	-	0.28	-	-	0.64	-	0.24	-	-	0.63	-	0.27	-	-
Cum. R ²	-	-	-	-	0.64	-	-	-	-	0.88	-	-	-	-	0.90

Notes: Weights and VIP scores indicate that wildfire had a significant negative effect on abundance of *N. fuscipes*, but no measurable effect on abundance of *P. maniculatus* or *S. occidentalis*; wildfire also had a significant negative effect on *N. fuscipes* tick burdens (due to absence of *N. fuscipes* from burned plots), but no measurable effect on tick burdens of *P. maniculatus* or *S. occidentalis* (except on the residual variation in *S. occidentalis* tick burdens). Partial least squares regression results for the effect of wildfire on *P. maniculatus*, *N. fuscipes*, and *S. occidentalis* abundance and *Ixodes pacificus* tick burdens in 2014 (1 yr post-fire). Results are presented as variable weights (wts), indicating direction of the effect, and VIP scores. Significant variables (VIP > 1) appear in boldface. R² values are for the full model (presented in Appendix S1: Tables S1 and S2).

end of the period of seasonal activity of *I. pacificus* in southern California (MacDonald and Briggs 2016), it is unlikely that a significant number of ticks were transported into the burn area by wide-ranging hosts, such as *O. h. californicus*, prior to tick sampling in winter and spring of the following year (2014). This suggests that any questing ticks collected in 2014 had survived the fire, likely in soil refugia (Padgett et al. 2009). Thus, in contrast to expectations that wildfires may cause direct tick mortality, both nymphal and adult *I. pacificus* ticks appear to have responded similarly to this wildfire as to prescribed burns in northern California where rates of survivorship in soil refugia were shown experimentally to be indistinguishable between burned and control plots (Padgett et al. 2009). Further, because wildfires largely occur during the dry summer months in California when *I. pacificus* is inactive in soil refugia, these observed patterns of abundance following wildfire may be consistent across burns in this region of the western United States. However, under changing climate conditions and increasing duration of annual fire seasons in California, this temporal mismatch between *I. pacificus* questing activity and dry-season wildfires may shift into the future resulting in different effects of fire on ticks and tick-borne disease ecology. Increases in abundance of questing adult and nymphal ticks in this study may have been due to these life stages failing to successfully locate hosts (Perkins

et al. 2006, Kilpatrick 2017), due to the reduced abundance of *O. h. californicus* and small vertebrate hosts within the burn extent. This increased abundance of vector ticks on the landscape may translate into higher risk of tick exposure and, potentially, elevated disease risk in the winter and spring immediately following summer wildfires in California in regions where rates of pathogen infection in tick populations are comparatively high. However, due to the dearth of infection in tick and host populations in this study, this remains an important open question.

In contrast, in the second and third years following the fire adult and nymphal tick, abundance declined substantially within the burn extent, suggesting a decrease in risk of tick exposure through time. Reduced adult and nymphal tick populations in years 2 and 3 following the fire could have been the result of lower nymphal and larval tick survivorship, respectively, over the summer dry season due to adverse abiotic conditions resulting from the fire. For example, there were clear changes in microhabitats and reduced vegetation cover within the burn perimeter, as well as significantly higher summer temperatures within the burn sites in the summer immediately preceding the observed declines in tick abundance. It is also possible that these observed reductions were due to fewer successful juvenile tick blood meals resulting from reduced host populations within the burn perimeter, or to reduced host acquisition as a

result of changes in vegetation structure that could have negatively affected tick questing behavior. Given comparable small vertebrate host populations, with the exception of *Neotoma fuscipes*, and immature tick burdens between burned and unburned sites in the year following the fire, adult and nymphal tick population reduction in years 2 and 3 was more likely the result of reduced survivorship over the summer dry season. Larval ticks appear to have been most directly impacted, leading necessarily to lower nymphal tick abundance in subsequent years. Again, these effects may have been the result of adverse abiotic conditions, such as elevated summer temperatures, leading to reduced survivorship over the summer dry season, or direct mortality of this particular life stage.

California mule deer (*O. h. californicus*) showed patterns of reduced activity within the fire perimeter in the first two years following the fire, recovering to levels comparable to adjacent unburned woodland by the third year. This slower recovery was unexpected, as new growth following fire has been shown to provide additional forage and initially attract large herbivores (Allan 2009). The observed pattern may have been due to the synergistic effect of wildfire and drought, which was impacting California throughout this study, leading to a more protracted recovery of pre-fire vegetation. Drought may have also reduced inter-annual tick survivorship within the burn area due to lack of suitable microhabitats and adverse abiotic conditions, like elevated temperature, resulting from loss of soil organic matter, duff, and herbaceous vegetation (Padgett and Lane 2001, Lane et al. 2009). Due to lower *O. h. californicus* activity within the fire perimeter, fewer adult tick blood meals and lower tick reproductive success would be expected to result from wildfire, reducing local tick populations, as observed.

The loss of *N. fuscipes*, an important pathogen reservoir (Lane and Brown 1991, Brown and Lane 1992, Foley et al. 2008, Swei et al. 2012), from sites impacted by wildfire is significant and mirrors earlier results from studies of prescribed burns in California (Padgett et al. 2009). Coupled with significantly reduced tick populations within the burn area, the loss of this pathogen reservoir could serve to reduce tick-borne disease risk for multiple years in oak woodlands

impacted by wildfire. Rates of infection with *Borrelia burgdorferi* s.l. in this study were extremely low, similar to the results of previous studies conducted in southern California (Lane et al. 2013, Padgett et al. 2014, Billeter et al. 2017, MacDonald et al. 2017), with infected nymphal ticks found only within the burn extent and only in the year following fire. With low sample sizes and insufficient variation in rates of infection to statistically assess the effect of wildfire on infection prevalence in vector ticks, the existence of such an effect merits further investigation. However, if wildfire serves initially to increase abundance of questing ticks on the landscape, particularly of the nymphal stage as observed in this study, this could lead to increased human contact with vector ticks, which could increase human disease risk in more highly endemic areas for tick-borne pathogen transmission in other regions of California. Thus, based on the results of this study, risk of tick exposure would be expected to increase in the winter and spring following summer wildfires and subsequently decline sharply for a minimum of two additional years in California oak woodlands impacted by fire. However, given the protracted life cycle of *I. pacificus* (Padgett and Lane 2001), tick populations are likely to be suppressed even longer due to time lags associated with slow transition from the juvenile stages to reproductive adults. These results convey key aspects of tick and vertebrate host ecology and response to fire that may be applicable to other regions in California where disease prevalence is higher.

The effects of forest perturbations have been the subject of much attention in the ecology of tick-borne disease in North America (Allan et al. 2003, LoGiudice et al. 2003, Brownstein et al. 2005, Jackson et al. 2006, Larsen et al. 2014, Seukep et al. 2015). However, unlike forest fragmentation resulting from human development (Allan et al. 2003, LoGiudice et al. 2003, Brownstein et al. 2005, Jackson et al. 2006, Larsen et al. 2014, Seukep et al. 2015) or sudden oak death (Swei et al. 2011b, 2012), destruction of forested habitats by wildfire is much more sudden and catastrophic, which may have very different effects on the ecology of tick-borne disease. Previous studies have found that controlled burns tend to reduce tick populations only temporarily (Hoch et al. 1972, Stafford et al. 1998, Cully 1999), but

that these effects do not last beyond the year of the burn (Stafford et al. 1998, Cully 1999). Other studies have even found an amplification of tick populations following fire, but burn frequency may modify these effects with higher frequency fires preventing population recovery (Davidson et al. 1994, Allan 2009). In one of the only studies conducted in the fire-prone western United States, Padgett et al. (2009) found that controlled burns in northern California reduced populations of rodent hosts, but had little overall effect on tick density. Adult *I. pacificus* survived fire in subsurface soil refugia and immature stages of *I. pacificus* were found infesting rodent hosts at similar or even higher densities in the prescribed burns as compared to unburned control plots (Padgett et al. 2009). These results have led to the conclusion that fire does not reduce tick abundance or tick-borne disease risk in California (Padgett et al. 2009), but our data show that the effect of wildfire differs fundamentally from prescribed burns and has the potential to have non-linear and long-lasting impacts on tick and key host populations in the transmission of tick-borne pathogens.

Given the results of earlier studies exploring the effects of controlled burns on tick and host populations, we expected that wildfire would have little effect on tick populations and tick-borne disease risk. In this study wildfire was found to have similar effects on tick and host populations in the year immediately following fire; questing tick abundance was elevated and *N. fuscipes* abundance was reduced within the burn extent, but other small vertebrate hosts and host tick burdens were not. However, we found that wildfire substantially reduced tick populations and tick exposure risk in subsequent years, with possible long-term reductions in risk due to (1) loss of reservoir hosts (*N. fuscipes*) from the system for a minimum of three years following the fire, (2) no observed change in populations of non-competent hosts (*Sceloporus occidentalis*), (3) slow recovery of reproductive hosts (*O. h. californicus*), and (4) substantial reductions in populations of the primary tick vector (*I. pacificus*) in the second and third years of the study, following initial increases in abundance of questing ticks.

While these clear differences between burned, experimental plots and unburned, control plots were both observed in the field and statistically

in the data, the lack of pre-fire data from this system makes these effects challenging to elucidate experimentally. Indeed, the unpredictable nature of catastrophic natural disturbances such as wildfire makes the ecological effects of such events nearly impossible to study experimentally. An experimental prescribed fire is highly unlikely to match the spatial scale and intensity of a large wildfire, and it is equally unlikely that a wildfire occurs on a landscape with ongoing monitoring of tick and host populations, leaving a balanced number of sampled plots burned and unburned. Short of such an unlikely scenario, we are left with quasi-experimental approaches, such as those employed in this study, and the potential that observed differences between "treatment" and "control" are due to other unobserved factors. For example, it is possible that the elevated abundance of ticks within the burn extent in the year following the fire was simply due to elevated abundance of ticks in this area prior to the fire. However, given the relative stability in tick populations across life stages in the unburned, control plots in this study, and that study plots were located in relatively close proximity in very similar habitats and topographies, the comparatively large changes in tick abundance through time in the burned plots were very likely due to the direct and/or indirect effects of the fire described above. Further, the finding that *N. fuscipes* were eliminated from within the burn extent in this study is consistent with earlier studies of prescribed burns in California (Padgett et al. 2009) and suggests a true effect of wildfire on this important reservoir species.

Beyond the implications of these findings for the ecology of ticks and tick-borne pathogens in California, and potential to alter patterns of human disease risk in disease endemic regions of the state, these results also have important implications for management of public lands in the state. The majority of fires occur on publicly owned and managed lands open to recreational activity and public use. For example, in the past ~30 yr, since Lyme disease became a notifiable disease in the United States, 62% of the total area burned in wildfires in California occurred on public lands (Appendix S1: Fig. S2). Further, heavily used recreation areas are often opened shortly after wildfires have been contained, and

certainly by the following winter and spring, unless there are major issues with slope erosion or recovery of sensitive habitat. Based on the results of this study, this potentially puts people at elevated risk of vector tick exposure. Following the White Fire, trails were officially reopened by 20 June, less than one month following this late spring wildfire, and were heavily used by hikers and for other recreational activities (A. J. MacDonald, *personal observation*) throughout the summer and following winter and spring when vector tick activity on the landscape was elevated. This scenario is likely often the case given that wildfires occur well before peak tick season the following winter and spring when people are likely to come into contact with ticks. Agencies managing these public lands, like the U.S. Forest Service or National and State Park Services, could use signage at trailheads and other recreation areas in regions with endemic Lyme, or other tick-borne diseases, that have experienced recent wildfires to indicate elevated risk of tick exposure, as this relationship is not intuitive and unlikely to be on the minds of the average recreator in California public lands.

Large-scale disturbances resulting from human activity and climate change are increasing in frequency and intensity (Dale 2001). As the pace of environmental change increases, resulting from changes in land use and climate, so too may the rate of emergence of zoonotic and vector-borne infectious disease (Patz et al. 2000, Jones et al. 2008, Lambin et al. 2010, Kilpatrick and Randolph 2012, Jones et al. 2013). It is therefore increasingly important for ecologists to study the impacts of disturbance and environmental change on human disease emergence and risk. In California, increasing understanding of the effects of wildfire, and potential interactions with climate change, on tick-borne disease risk is thus of critical importance. In this study, we find that wildfire results in elevated risk of tick encounter and, potentially, tick-borne disease risk immediately following fire, but that risk is subsequently reduced substantially for multiple years into the future.

ACKNOWLEDGMENTS

We would like to thank Dr. Hillary Young, Dr. Tom Dudley, Dr. Ashley Larsen, and four anonymous

reviewers for comments and suggestions on earlier drafts of this manuscript. We also thank Valerie Hubbartt, the Santa Barbara Ranger District, and USDA Forest Service for access to the Los Padres National Forest to conduct this research. Funding was provided by the Department of Ecology, Evolution and Marine Biology block grant (to AJM), the UC Institute for the study of Ecological and Evolutionary Climate Impacts Fellowship (to AJM), and the Worster family and Worster Award (to AJM and DWH). We thank Tyler Toth, Narek Ohanian, John Brewington, Sarah Russ, Negeen Izadian, Aybuke Koyuncu, and Kelsie Bogyo for help in the field. Animal use was in accordance with University of California, Santa Barbara IACUC protocol #863, and California Department of Fish and Wildlife Scientific Collecting Permit, SC-12329.

LITERATURE CITED

- Allan, B. F. 2009. Influence of prescribed burns on the abundance of *Amblyomma americanum* (Acari: Ixodidae) in the Missouri Ozarks. *Journal of Medical Entomology* 46:1030–1036.
- Allan, B. F., F. Keesing, and R. S. Ostfeld. 2003. Effect of forest fragmentation on Lyme disease risk. *Conservation Biology* 17:267–272.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348–358.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Benedict, M. Q., R. S. Levine, W. A. Hawley, and L. P. Lounibos. 2007. Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. *Vector-Borne and Zoonotic Diseases* 7:76–85.
- Billeter, S. A., M. H. Yoshimizu, and R. Hu. 2017. Species composition and temporal distribution of adult ixodid ticks and prevalence of *Borrelia burgdorferi* sensu lato and *Rickettsia* species in Orange County, California. *Journal of Vector Ecology* 42:189–192.
- Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soule. 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7:552–563.
- Brown, R. N., and R. S. Lane. 1992. Lyme disease in California: a novel enzootic transmission cycle of *Borrelia burgdorferi*. *Science* 256:1439–1442.

- Brownstein, J. S., D. K. Skelly, T. R. Holford, and D. Fish. 2005. Forest fragmentation predicts local scale heterogeneity of Lyme disease risk. *Oecologia* 146:469–475.
- Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Carrascal, L. M., I. Galván, and O. Gordo. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos* 118:681–690.
- Casher, L., R. Lane, R. Barrett, and L. Eisen. 2002. Relative importance of lizards and mammals as hosts for ixodid ticks in northern California. *Experimental and Applied Acarology* 26:127–143.
- Collins, B. M., D. L. Fry, J. M. Lydersen, R. Everett, and S. L. Stephens. 2017. Impacts of different land management histories on forest change. *Ecological Applications* 27:2475–2486.
- Cully Jr., J. F. 1999. Lone star tick abundance, fire, and bison grazing in tallgrass prairie. *Journal of Range Management* 52:139–144.
- Dale, V. H., et al. 2001. Climate change and forest disturbances. *BioScience* 51:723–734.
- Davidson, W. R., D. A. Sieffken, and L. H. Creekmore. 1994. Influence of annual and biennial prescribed burning during March on the abundance of *Amblyomma americanum* (Acari: Ixodidae) in central Georgia. *Journal of Medical Entomology* 31:72–81.
- Eisen, R. J., L. Eisen, M. B. Castro, and R. S. Lane. 2003. Environmentally related variability in risk of exposure to Lyme disease spirochetes in northern California: effect of climatic conditions and habitat type. *Environmental Entomology* 32:1010–1018.
- Eisen, R. J., L. Eisen, and R. S. Lane. 2001. Prevalence and abundance of *Ixodes pacificus* immatures (Acari: Ixodidae) infesting western fence lizards (*Sceloporus occidentalis*) in northern California: temporal trends and environmental correlates. *Journal of Parasitology* 87:1301–1307.
- Eisen, R. J., L. Eisen, and R. S. Lane. 2006. Predicting density of *Ixodes pacificus* nymphs in dense woodlands in Mendocino County, California, based on geographic information systems and remote sensing versus field-derived data. *American Journal of Tropical Medicine and Hygiene* 74:632–640.
- Eshoo, M. W., H. E. Carolan, C. Massire, D. M. Chou, C. D. Crowder, M. A. Rounds, C. A. Phillipson, S. E. Schutzer, and D. J. Ecker. 2015. Survey of *Ixodes pacificus* ticks in California reveals a diversity of microorganisms and a novel and widespread Anaplasmataceae species. *PLoS ONE* 10:e0135828–14.
- Foley, J. E., N. C. Nieto, J. Adjemian, H. Dabritz, and R. N. Brown. 2008. *Anaplasma phagocytophilum* infection in small mammal hosts of *Ixodes* ticks, western United States. *Emerging Infectious Diseases* 14:1147–1150.
- Gleim, E. R., L. M. Conner, R. D. Berghaus, M. L. Levin, G. E. Zemtsova, and M. J. Yabsley. 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.
- Hamm, K. A., L. V. Diller, and D. W. Kitchen. 2002. Comparison of indices to estimate abundance of dusky-footed woodrats. *Wildlife Society Bulletin* 30:64–70.
- Hoch, A. L., P. J. Semtnar, R. W. Barker, and J. A. Hair. 1972. Preliminary observations on controlled burning for lone star tick (Acarina: Ixodidae) control in woodlots. *Journal of Medical Entomology* 9:446–451.
- Horak, I. G., G. J. Gallivan, A. M. Spickett, and A. L. F. Potgieter. 2006. Effect of burning on the numbers of questing ticks collected by dragging. *Onderstepoort Journal of Veterinary Research* 73:163–174.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133–140.
- Jackson, L. E., E. D. Hilborn, and J. C. Thomas. 2006. Towards landscape design guidelines for reducing Lyme disease risk. *International Journal of Epidemiology* 35:315–322.
- Jones, B. A., et al. 2013. Zoonosis emergence linked to agricultural intensification and environmental change. *Proceedings of the National Academy of Sciences* 110:8399–8404.
- Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman, and P. Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451:990–993.
- Kilpatrick, A. M., et al. 2017. Lyme disease ecology in a changing world: consensus, uncertainty and critical gaps for improving control. *Philosophical Transactions of the Royal Society B* 372:20160117–15.
- Kilpatrick, A. M., and S. E. Randolph. 2012. Drivers, dynamics, and control of emerging vector-borne zoonotic diseases. *Lancet* 380:1946–1955.
- Lambin, E. F., A. Tran, and S. O. Vanwambeke. 2010. Pathogenic landscapes: interactions between land, people, disease vectors, and their animal hosts. *International Journal of Health Geographics* 9: 1–13.
- Lane, R. S., and R. N. Brown. 1991. Wood rats and kangaroo rats: potential reservoirs of the Lyme disease spirochete in California. *Journal of Medical Entomology* 28:299–302.
- Lane, R. S., and W. Burgdorfer. 1986. Potential role of native and exotic deer and their associated ticks (Acari: Ixodidae) in the ecology of Lyme disease in

- California, USA. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene, Series A: Medical Microbiology, Infectious Diseases, Virology, Parasitology* 263:55–64.
- Lane, R. S., N. Fedorova, J. E. Kleinjan, and M. Maxwell. 2013. Eco-epidemiological factors contributing to the low risk of human exposure to ixodid tick-borne borreliae in southern California, USA. *Ticks and Tick-borne Diseases* 4:377–385.
- Lane, R. S., J. Mun, R. J. Eisen, and L. Eisen. 2005. Western gray squirrel (Rodentia: Sciuridae): A primary reservoir host of *Borrelia burgdorferi* in Californian oak woodlands? *Journal of Medical Entomology* 42:388–396.
- Lane, R. S., J. Mun, and H. A. Stubbs. 2009. Horizontal and vertical movements of host-seeking *Ixodes pacificus* (Acari: Ixodidae) nymphs in a hardwood forest. *Journal of Vector Ecology* 34:252–266.
- Lane, R. S., and G. B. Quistad. 1998. Borreliacidal factor in the blood of the western fence lizard (*Sceloporus occidentalis*). *Journal of Parasitology* 84:29–34.
- Lane, R. S., D. B. Steinlein, and J. Mun. 2004. Human behaviors elevating exposure to *Ixodes pacificus* (Acari: Ixodidae) nymphs and their associated bacterial zoonotic agents in a hardwood forest. *Journal of Medical Entomology* 41:239–248.
- Larsen, A. E., A. J. MacDonald, and A. J. Plantinga. 2014. Lyme disease risk influences human settlement in the wildland-urban interface: evidence from a longitudinal analysis of counties in the northeastern United States. *American Journal of Tropical Medicine and Hygiene* 91:747–755.
- Lawler, J. J., D. J. Lewis, E. Nelson, A. J. Plantinga, S. Polasky, J. C. Withey, D. P. Helmers, S. Martinuzzi, D. Pennington, and V. C. Radeloff. 2014. Projected land-use change impacts on ecosystem services in the United States. *Proceedings of the National Academy of Sciences* 111:7492–7497.
- Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* 47:278–291.
- LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences USA* 100:567–571.
- MacDonald, A. J., and C. J. Briggs. 2016. Truncated seasonal activity patterns of the western blacklegged tick (*Ixodes pacificus*) in central and southern California. *Ticks and Tick-borne Diseases* 7:234–242.
- MacDonald, A. J., D. W. Hyon, J. B. Brewington, K. E. O'Connor, A. Swei, and C. J. Briggs. 2017. Lyme disease risk in southern California: abiotic and environmental drivers of *Ixodes pacificus* (Acari: Ixodidae) density and infection prevalence with *Borrelia burgdorferi*. *Parasites & Vectors* 10:7.
- McDonald, T. 2015. mra: analysis of mark-recapture data. R package version 2.16.4. <https://cran.r-project.org/web/packages/mra/mra.pdf>
- Neary, D. G., C. C. Klopatek, L. F. DeBano, and P. F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122:51–71.
- North, M. P., and M. D. Hurteau. 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. *Forest Ecology and Management* 261:1115–1120.
- Padgett, K., D. Bonilla, A. Kjemtrup, I.-M. Vilcins, M. H. Yoshimizu, L. Hui, M. Sola, M. Quintana, and V. Kramer. 2014. Large scale spatial risk and comparative prevalence of *Borrelia miyamotoi* and *Borrelia burgdorferi* sensu lato in *Ixodes pacificus*. *PLoS ONE* 9:e110853.
- Padgett, K. A., L. E. Casher, S. L. Stephens, and R. S. Lane. 2009. Effect of prescribed fire for tick control in California chaparral. *Journal of Medical Entomology* 46:1138–1145.
- Padgett, K. A., and R. S. Lane. 2001. Life cycle of *Ixodes pacificus* (Acari: Ixodidae): timing of developmental processes under field and laboratory conditions. *Journal of Medical Entomology* 38:684–693.
- Patz, J. A., T. K. Graczyk, N. Geller, and A. Y. Vittor. 2000. Effects of environmental change on emerging parasitic diseases. *International Journal for Parasitology* 30:1395–1405.
- Perkins, S. E., I. M. Cattadori, V. Tagliapietra, A. P. Rizzoli, and P. J. Hudson. 2006. Localized deer absence leads to tick amplification. *Ecology* 87:1981–1986.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roberts, D. A., P. E. Dennison, S. Peterson, S. Sweeney, and J. Rechel. 2006. Evaluation of airborne visible/infrared imaging spectrometer (AVIRIS) and moderate resolution imaging spectrometer (MODIS) measures of live fuel moisture and fuel condition in a shrubland ecosystem in southern California. *Journal of Geophysical Research: Biogeosciences* 111:G04S02.
- Rowland, M. M., G. C. White, and E. M. Karlen. 1984. Use of pellet-group plots to measure trends in deer and elk populations. *Wildlife Society Bulletin* 12:147–155.
- Salkeld, D. J., and R. S. Lane. 2010. Community ecology and disease risk: lizards, squirrels, and the Lyme disease spirochete in California, USA. *Ecology* 91:293–298.
- Salkeld, D. J., S. Leonhard, Y. A. Girard, N. Hahn, J. Mun, K. A. Padgett, and R. S. Lane. 2008.

- Identifying the reservoir hosts of the Lyme disease spirochete *Borrelia burgdorferi* in California: the role of the western gray squirrel (*Sciurus griseus*). American Journal of Tropical Medicine and Hygiene 79:535–540.
- Sanchez, G. 2012. plsdepot: partial least squares (PLS) data analysis methods. R package version 0.1.17. <https://CRAN.R-project.org/package=plsdepot>
- Scifres, C. J., T. W. Oldham, P. D. Teel, and D. L. Drawe. 1988. Gulf Coast tick (*Amblyomma maculatum*) populations and responses to burning of coastal prairie habitats. Southwestern Naturalist 33:55–64.
- Seukep, S. E., K. N. Kolivras, Y. Hong, J. Li, S. P. Prisley, J. B. Campbell, D. N. Gaines, and R. L. Dymond. 2015. An examination of the demographic and environmental variables correlated with Lyme disease emergence in Virginia. Eco-Health 12:634–644.
- Smith, A., B. Meulders, C. M. Bull, and D. Driscoll. 2012. Wildfire-induced mortality of Australian reptiles. Herpetology Notes 5:233–235.
- Spickett, A. M., I. G. Horak, A. Van Niekerk, and L. E. Braack. 1992. The effect of veld-burning on the seasonal abundance of free-living ixodid ticks as determined by drag-sampling. Onderstepoort Journal of Veterinary Research 59:285–292.
- Stafford, K. C., J. S. Ward, and L. A. Magnarelli. 1998. Impact of controlled burns on the abundance of *Ixodes scapularis* (Acari: Ixodidae). Journal of Medical Entomology 35:510–513.
- Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:8.
- Stephens, S. L., R. E. Martin, and N. E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251:205–216.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.
- Swei, A., C. J. Briggs, R. S. Lane, and R. S. Ostfeld. 2012. Impacts of an introduced forest pathogen on the risk of Lyme disease in California. Vector-Borne and Zoonotic Diseases 12:623–632.
- Swei, A., R. Meentemeyer, and C. J. Briggs. 2011a. Influence of abiotic and environmental factors on the density and infection prevalence of *Ixodes pacificus* (Acari: Ixodidae) with *Borrelia burgdorferi*. Journal of Medical Entomology 48:20–28.
- Swei, A., R. S. Ostfeld, R. S. Lane, and C. J. Briggs. 2011b. Effects of an invasive forest pathogen on abundance of ticks and their vertebrate hosts in a California Lyme disease focus. Oecologia 166:91–100.
- Tietje, W. D., J. K. Vreeland, N. R. Siepel, and J. Dockter. 1997. Relative abundance and habitat associations of vertebrates in oak woodlands in coastal-central California. Pages 391–400 in N. H. Pillsbury, J. Verner, and W. D. Tietje, technical coordinators. Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues; 19–22 March 1996; San Luis Obispo, CA. General Technical Report PSW-GTR-160. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California, USA.
- Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B 371:20150178.
- Westerling, A. L., and B. P. Bryant. 2007. Climate change and wildfire in California. Climatic Change 87:231–249.
- Westerling, A. L., B. P. Bryant, H. K. Preisler, T. P. Holmes, H. G. Hidalgo, T. Das, and S. R. Shrestha. 2011. Climate change and growth scenarios for California wildfire. Climatic Change 109:445–463.
- White, G. C., and L. E. Eberhardt. 1980. Statistical analysis of deer and elk pellet-group data. Journal of Wildlife Management 44:121–131.
- Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in R. Journal of Statistical Software. <https://doi.org/10.18637/jss.v027.i08>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2227/full>