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Modeling future climate suitability for the western blacklegged tick, *Ixodes pacificus*, in California with an emphasis on land access and ownership

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Abstract

In the western United States, *Ixodes pacificus* Cooley & Kohls (Acari: Ixodidae) is the primary vector of the agents causing Lyme disease and granulocytic anaplasmosis in humans. The geographic distribution of the tick is associated with climatic variables that include temperature, precipitation, and humidity, and biotic factors such as the spatial distribution of its primary vertebrate hosts. Here, we explore (1) how climate change may alter the geographic distribution of *I. pacificus* in California, USA, during the 21st century, and (2) the spatial overlap among predicted changes in tick habitat suitability, land access, and ownership. Maps of potential future suitability for *I. pacificus* were generated by applying climate-based species distribution models to a multi-model ensemble of climate change projections for the Representative Concentration

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Author Statement of Data Accessibility
Tick presence locations were obtained from the California Department of Public Health and are not publicly available because the dataset contains protected personal information. The climate data used in these study were derived from two publicly available datasets described in detail in the manuscript (MACAv2-LIVNEH and Daymet). The value-added 1-km climate rasters used in the study are available upon request.

Supplementary materials
Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2021.101789.

Pathway (RCP) 4.5 (moderate emission) and 8.5 (high emission) scenarios for two future periods: mid-century (2026–2045) and end-of-century (2086–2099). Areas climatically-suitable for *I. pacificus* are projected to expand by 23% (mid-century RCP 4.5) to 86% (end-of-century RCP 8.5) across California, compared to the historical period (1980–2014), with future estimates of total suitable land area ranging from about 88 to 133 thousand km^2, or up to about a third of California. Regions projected to have the largest area increases in suitability by end-of-century are in northwestern California and the south central and southern coastal ranges. Over a third of the future suitable habitat is on lands currently designated as open access (i.e. publicly available), and by 2100, the amount of these lands that are suitable habitat for *I. pacificus* is projected to more than double under the most extreme emissions scenario (from ~23,000 to >51,000 km^2). Of this area, most is federally-owned (>45,000 km^2). By the end of the century, 26% of all federal land in the state is predicted to be suitable habitat for *I. pacificus*. The resulting maps may facilitate regional planning and preparedness by informing public health and vector control decision-makers.

Keywords

Ixodes pacificus; Habitat modeling; Climate change; Land ownership; Lyme disease; California

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1. Introduction

In the western United States, the western blacklegged tick, *Ixodes (I.) pacificus* Cooley & Kohls, is the primary vector to humans of the Lyme disease spirochete *Borrelia burgdorferi* sensu stricto (Burgdorfer et al., 1985; Lane et al., 1994). It is also an important vector of *Anaplasma phagocytophilum*, the causal pathogen of human granulocytic anaplasmosis (Teglas and Foley, 2006), and is considered a probable vector of *B. miyamotoi* (Krause et al., 2018; Mun et al., 2006; Padgett et al., 2014; Scoles et al., 2001). While human cases of Lyme disease and anaplasmosis are more prevalent in northwestern counties of California and in the foothills of the Sierra Nevada, *I. pacificus* is broadly distributed across the state (Eisen et al., 2006; Lane et al., 1992; Padgett et al., 2014; Yoshimizu et al.2016). *Ixodes pacificus* has been collected in 56 of 58 Californian counties, but local abundance varies (Dennis et al., 1998; Eisen et al., 2006; Eisen et al., 2016; MacDonald and Briggs, 2016; Salkeld et al., 2014).

Previous tick distribution models, grounded on climatic and land cover variables, have characterized the contemporary geographic range of *I. pacificus* in the western U.S. (Eisen et al., 2018; Hahn et al., 2016; Porter et al., 2021). Hahn et al. (2016) developed an ensemble of four county-level species distribution models for *I. pacificus* across the West, which indicated broad suitability for the tick in California at this spatial resolution. Temperature and percentage forest cover contributed to suitability; however, precipitation seasonality was a particularly important explanatory variable across the models, suggesting that areas with distinct wet and dry seasons are most suitable (Hahn et al., 2016). The amount of cold season precipitation (generally the wettest period of year in much of California) is also an important contributor to suitability across the models, with increasing suitability as the average precipitation within a county increases from 200 to 500 mm (Hahn et al., 2016).

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Previously, we developed an ensemble of five species distribution models for *I. pacificus*, but focused specifically on California at high (1 km) spatial resolution (Eisen et al., 2018). The models predict broad suitability for *I. pacificus* in both northern and southern California, but compared to Hahn et al. (2016), the patterns of suitability are more complex by indicating only small pockets of suitability in the western portions of larger arid counties in southern California. The most important explanatory climatic variables across models were cold-season temperature and rainfall; areas having relatively warm and wet winters, such as central California, were predicted to be most suitable for *I. pacificus*. Most recently, a study using a similar ecological niche modeling approach with tick presence records collected through a citizen science program across California, Oregon, and Washington, found that increasing average vapor pressure in the spring, isothermality, and percent forest cover were the strongest predictors of suitability for *I. pacificus* in these western states (Porter et al., 2021).

Using species distribution models to project how 21st century climate change may impact the future geographic distribution of *I. pacificus* can inform public health planning and preparedness, particularly for areas where the tick is projected to emerge. To date, only one study has investigated the possible impacts of climate change on the geographic distribution of *I. pacificus* (Porter et al., 2021), predicting that increases in temperature seasonality may lead to a 30% decrease in suitable land area for the tick across the West. In contrast, numerous authors have assessed how climate change may affect the range of *I. scapularis* across the eastern U.S. (Brownstein et al., 2005) and southern Canada (Leighton et al., 2012; Ogden et al., 2008, 2006; Simon et al., 2014). A number of the models were driven solely by temperature-based variables, though some included temperature and precipitation covariates. Taken together, the studies predict an expansion of *I. scapularis* into more northerly latitudes (mainly in Canada) and higher altitudes due to warmer temperatures, and a contraction of *I. scapularis* at its southernmost margins in the southeastern U.S.

Near-surface air temperatures are projected to increase across California throughout the 21st century, and conditions across much of the state are projected to become drier due to altered precipitation patterns and/or increased drying due to warming (Bedsworth et al., 2018). In turn, these climatic changes may impact the spatial distribution of *I. pacificus* in complex ways (Eisen et al., 2015). Our objectives in this study were twofold. First, we employed the species distribution models of Eisen et al. (2018) to explore how the suitable geographic range for *I. pacificus* in California may evolve throughout the 21st century under two plausible climate change scenarios: a low-to-moderate emissions and concentration scenario and a high-emissions and concentration scenario. Second, we assessed the spatial overlap between modeled changes in tick habitat suitability, land access, and ownership. Much of the California land area is protected for public use by more than 1,000 public agencies or non-profit organizations. These publicly available lands provide outdoor recreational areas for Californian residents and visitors, and expansion of suitable tick habitat in these areas may be a particularly important driver of increased human exposure to ticks.

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2. Materials and Methods

2.1. Present day species distribution models

This paper builds on earlier work by our team (Eisen et al., 2018) to develop an ensemble species distribution model to predict the probability for *I. pacificus* distribution in present-day California, restricting the modeled results to land cover classes where ticks are typically encountered, i.e., forest, grass, scrub-shrub, and riparian. Briefly, we used 621 *I. pacificus* (all life stages) presence locations distributed across 51 counties as presence points Eisen et al. 2018) to develop five species distribution models: 1) boosted regression trees (BRT), 2) generalized linear model (GLM), 3) multivariate adaptive regression spline (MARS), 4) maximum entropy (Maxent), and 5) random forest (RF). Candidate predictors in that modeling process included 35 climate variables selected based on our knowledge of the biological and ecological requirements of *I. pacificus* and include 19 bioclimatic variables (Hijmans et al., 2005), and average seasonal day length, growing degree days, and vapor pressure. Collinear variables were reduced by retaining the variable from collinear pairs that explained the most variance in the model or that were deemed the most biologically meaningful. Models were validated using AUC (Area Under the Receiver-Operator Curve), and the resulting continuous probability maps were used to create binary habitat suitability maps employing the probability threshold that produced estimates with 90% sensitivity (Hahn et al., 2017). We created an ensemble prediction by summing the binary maps, and our results highlighted areas along the northern coast and the western Sierra Nevada foothills as highly suitable for *I. pacificus*.

2.2. Future climate change projections

Monthly 1/16th degree spatial resolution climate projections for maximum temperature, minimum temperature, precipitation and specific humidity were obtained from the MACAv2-LIVNEH dataset from Northwest Climate Science Center (Northwest Climate Science Center, 2020). The MACAv2-LIVNEH data were developed by statistically downscaling global climate model (GCM) data from the Coupled Model Intercomparison Project 5 (CMIP5, Taylor et al., 2012). Statistical downscaling in the present context is a method whereby statistical relationships are developed between coarse resolution data from GCM simulations and finer resolution data based on meteorological observations (“training data”), and then those relationships are applied to the coarse GCM data to “downscale” it to the a higher-resolution local scale that is relevant for, e.g., habitat suitability studies (Benestad et al., 2008). The MACAv2-LIVNEH climate dataset was derived utilizing a modification of the Multivariate Adaptive Constructed Analogs (MACA, Abatzoglou and Brown, 2012) method with the Livneh observational dataset as training data (Livneh et al., 2015).

Five GCMs were selected from the database according to the following three criteria: (1) they had simulations available for all time periods and emissions scenarios of interest (see below); (2) they ranked among the top of the CMIP5 GCMs in their ability to simulate observed temperature and rainfall globally according to Knutti et al. (2013); (3) they each came from a different model genealogy according to Knutti et al. 2013), ensuring that each model is sufficiently unique from the others. The five selected GCMs were: Second

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Generation Canadian Earth System Model (CanESM2, Canada); Community Climate System Model version 4 (CCSM4; United States); Geophysical Fluid Dynamics Laboratory Earth System Model with Modular Ocean Model4 component (GFDL-ESM2M United States); Hadley Centre Global Environment Model version 2- Earth System (HadGEM2-ES United Kingdom); and Model for Interdisciplinary Research on Climate version 5 (MIROC5, Japan).

The GCM simulations were obtained for the historical period (1990– 2005) and two future time periods (2026–2045 and 2086–2099). The future simulations were obtained for two Representative Concentration Pathway (RCP, van Vuuren et al., 2011) scenarios: RCP4.5 and RCP8.5. RCP4.5 is a low-to-moderate emissions and concentration scenario with GHG radiative forcing reaching 4.5 W m^{-2} near 2100. RCP4.5 represents a trajectory that may be plausible if international actions are taken to stabilize and reduce GHG emissions (Thomson et al., 2011), though global average warming by 2100 under RCP4.5 is still projected to be ~2.5°C above pre-industrial times, more than the threshold goal of 1.5–2.0°C set under the Paris Agreement (Sanderson et al., 2016). RCP8.5 is a high-emissions and concentration scenario with GHG radiative forcing reaching 8.5 W m^{-2} near 2100. RCP8.5 represents a plausible trajectory if little is done to curb greenhouse gas emissions (Riahi et al., 2011).

An ensemble mean was constructed by averaging each variable from all five GCMs. Significant bioclimatic variables from Eisen et al.(2018) (isothermality (BIO3), maximum temperature of the warmest month (BIO5), mean temperature of the coldest quarter (BIO11), precipitation seasonality (BIO15), precipitation of the warmest quarter (BIO18), precipitation of the coldest quarter (BIO19)) were then computed for each GCM and the ensemble mean using monthly maximum temperature, minimum temperature and precipitation; this step was done with the ‘dismo’ package (v1.3–3, Hijmans et al., 2020) in R v3.4.0. The autumn (September-November average) specific humidity variable from each GCM and the ensemble mean was converted to the vapor pressure variable required by the *I. pacificus* model from Eisen et al. (2018) using a standard humidity conversion equation for vapor pressure as a function of mixing ratio (specific humidity≈mixing ratio) and surface pressure (whereby surface pressure was estimated across California from the elevation and historical autumn near-surface temperature using the hypsometric equation).

Next, the climate change “deltas” for each of these variables were computed by either subtracting or dividing the future GCM variable value by its historical (1990–2005) GCM value. The temperature and vapor pressure variables were subtracted (BIO5, BIO11 and VP), whereas the variables expressed as percentages and the precipitation variables were divided (BIO3, BIO15, BIO18 and BIO19). These change variables were then remapped with a distance-weighted algorithm to the 1-km historical (1980–2014) Daymet (Thorton et al., 2012) grid that was used to generate the *I. pacificus* model in Eisen et al. (2018) and added or multiplied by their respective historical Daymet variables. In this manner, we generated climate change projections for the four future periods and two RCP scenarios that were calibrated to the 1980–2014 historical Daymet fields in Eisen et al. (2018). Note that the GCM historical period (1990–2005) is centered within the Daymet historical period (1980–2014) such that the deltas computed from the GCM historical period are likely to be consistent with the Daymet historical period (i.e., the changes are temporally realistic).

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2.3. Predicting future habitat suitability for Ixodes pacificus

We projected the current distribution results from the five models (BRT, GLM, MARS, Maxent, RF) using ensemble mean values under two climate scenarios (RCP4.5 and RCP8.5), over two time ranges: mid-century (2026–2045) and end-of-century (2086–2099). Binary habitat suitability maps were developed from the continuous habitat suitability probability output using a threshold that produced predictions with 90% sensitivity. We restricted the output to land cover in which ticks are found (i.e., forest, grass, scrub-shrub, riparian) by overlaying the California vegetation layer developed by the California Department of Forestry and Fire Protection (FRAP) (http://frap.fire.ca.gov/data/frapgis-data-sw-fveg_download). Next, we summed the five binary suitability maps (BRT, GLM, MARS, Maxent, RF) for each time period and emissions scenario and identified areas that were classified as suitable habitat in the future in three or more models. The binary future suitable/unsuitable habitat maps were compared to the map of current suitable/unsuitable habitat to create four change categories: 1) suitable in both time periods, 2) habitat gained, 3) habitat lost, and 4) unsuitable in both time periods under four climate scenarios (Figure 1, Objective 1). Future suitable habitat is the sum of suitable in both time periods and habitat gained, and future unsuitable habitat is the sum of suitable habitat lost and unsuitable in both time periods (Figure 1).

To evaluate uncertainty in our future predictions, we created an ensemble Multivariate Environmental Similarity Surface (MESS) map for each of the four ensemble prediction maps (two periods, under two climate scenarios) by summing MESS scores across the five modeled predictions. Using this method, each pixel was assigned a consensus MESS score (range = 0–5). A score of 0 indicates that future climatic conditions in the pixel did not fall outside the range of historically observed conditions in any of the five GCMs (i.e., no extrapolation, high confidence). In contrast, a score of 5 indicates that future climatic conditions fell outside the range of historically observed conditions in all five GCMs (i.e., extensive extrapolation, low confidence). We used the Software for Assisted Habitat Modeling (USGS) for habitat modeling. Other analyses were completed using Jupyter Notebooks and the ArcPy module in ESRI ArcGIS Pro.

2.4. Future habitat suitability of open access land in California

The four change categories: suitable in both time periods, habitat gained, habitat lost, and unsuitable in both time periods under four climate scenarios were intersected with the California Protected Areas Database (CPAD) to investigate the land access status of modeled habitat suitability for *I. pacificus* (Fig. 1, Objective 2.1). Specifically, we identified areas that were shown to be climatically suitable for *I. pacificus* under future climate scenarios (i.e. suitable in both time periods and habitat gained) and were on “open access” land, meaning that it is available for public use. Once we identified areas that met both criteria (climatically suitable habitat and on open access land), we investigated land ownership of these areas (e.g. Federal, State, City, Special District, Non Profit, County, and Private) (Fig. 1, Objective 2.2). By identifying areas where open access land may contain future suitable habitat for *I. pacificus*, and by understanding who owns these lands, we can identify high priority areas for intervention to decrease human exposure to ticks. CPAD is a GIS dataset depicting lands that are owned and protected for open space purposes by more than 1,000 public agencies

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or non-profit organizations (GreenInfo Network 2021). CPAD includes a wide diversity of parks and open spaces in California, ranging from national forests, national parks, state parks, county open spaces, and neighborhood pocket parks.

3. Results

3.1. Projections of future suitability for Ixodes pacificus

The pattern of modeled future suitable habitat for *I. pacificus* in California across RCP scenarios was largely consistent with the models of current habitat in Eisen et al. (2018) (Fig. 2, Fig. A.1). Across all time periods and RCPs, our models predict suitable habitat in the north coast region, Klamath and Cascade ranges into the Sierra Nevada mountains, in the San Francisco Bay Area, and south central coast through the Transverse Ranges.

At present, 17.4% of the land area in California (~72 thousand km^2) is suitable habitat for *I. pacificus* (Eisen et al. 2018). Modeled results suggest a substantial increase in suitable habitat across the state, with future estimates of total suitable land area ranging from about 88 to 133 thousand km^2, or up to a third of California, representing a 23 to 88% increase in suitable habitat area in the state across climate change scenarios. (Table 1). Overall, suitable habitat is predicted to expand in the northwestern region, in the Sierra Nevada foothills, and along the southern coastal and Transverse ranges under both emissions scenarios (Fig. 3). The expansion of newly suitable habitat becomes more pronounced in the latter half of the century, particularly under RCP 8.5 with more suitable land area in northwestern California and the south central coast. The end-of-century projections under RCP 4.5 show a small area of lost tick habitat in southern California, but this region becomes more suitable under the high emissions scenario over the same time period. The only other area where tick habitat is predicted to contract is a small region in north central California under the end-of-century high emissions scenario.

In the ensemble MESS maps, the greatest uncertainty in future projections of habitat suitability were in southern California (Fig. 4). Under RCP 4.5, the highest levels of uncertainty (consensus MESS scores of 4 or 5) were concentrated on the southern California coast between Los Angeles and San Diego and along the southern California-Mexico border with a small area of high uncertainty in Death Valley. There was more uncertainty in projections under RCP 8.5. There was high uncertainty for the projections along the coast south of Monterey, in most of southern California south of Los Angeles, and in a few locations in the central part of the state. Despite these areas of high uncertainty in southern California, more than 86% (range: 86.9 to 99.2%, depending on scenario) of the land area in California had consensus MESS scores = 0. That is, none of the GCMs predicted future climate variables outside of the historical range used to train the habitat models, indicating high certainty in the projections in these areas.

3.2. Climate variables driving habitat changes

Although it is difficult to isolate the effect of single climate variables on the predicted changes in *I. pacificus* habitat, combining information from the response curves linking climate variables and suitability with maps of contemporary and future climate variables can

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facilitate interpretation of the suitability results (Fig. A.2–A.4). Two variables, cold season precipitation (Bio 19) and cold season mean temperature (Bio 11) explain approximately 50 to 100% of the variability in all five ecological niche models in Eisen et al. (2018). Therefore, we focus on changes in these two variables as potential drivers of future suitability for *I. pacificus*. In addition, because the model results based on RCP 4.5 mirror those from RCP 8.5 but with more modest changes, we focus our interpretation on the more extreme scenario where changes in habitat suitability are more apparent. In the models of future *I. pacificus* habitat, we observed the most substantial habitat expansion in the central coast and Northwestern California, so again, we limited our interpretation primarily to these geographic regions.

Based on the variable response curves from the contemporary models of tick habitat suitability from Eisen et al. (2018) (Fig. A.2), we observed increasing suitability between average values of 10 to 400 mm, with fairly little change in suitability for values higher than 400 mm. Most areas in Northwestern California already exceed the upper threshold of 400 mm in the present day (Fig. A.3), so cold season precipitation is likely not a substantial contributor to predictor increases in suitability in this region. In contrast, the central coast of California currently experiences drier winters (mostly <400 mm on average) but is predicted to experience substantial increases in winter precipitation under all climate scenarios (Fig. A.4), which is likely a primary driver of increased habitat suitability in this region.

The response curves of cold season mean temperature from Eisen et al. (2018) shows increasing habitat suitability for *I. pacificus* between the range of approximately −2 and 5°C (Figure A.2). Although cold season mean temperature is projected to increase across the state of California under future climate scenarios (Figure A.4), this variable is likely one of the most important contributors to increasing suitability in Northwestern California, a region that currently stays below 5°C during the winter months (Figure A.3). This contrasts from the central coast of the state where winter temperatures are regularly above 5°C and are therefore not a limiting factor for habitat suitability in the region. The only area where models predicted decreasing habitat suitability is in southern California, which is an area where the MESS maps indicated high uncertainty in the model predictions.

3.3. Habitat expansion on open access land and land ownership

California’s land area is roughly evenly split between land with open access (193,761 km^2, 47%) and non-open access (215,680 km^2, 53%). When the modeled change maps were overlaid with data showing land access status, we found that over a third of the future suitable tick habitat was on open access land across all scenarios. Additionally, by the end of the century, the amount of open access land area that is suitable habitat for *I. pacificus* is projected to more than double under the most extreme emissions scenario (from 23,363 km^2 in the present day compared to $>$51,000 km^2 in the future) (Table 2).

Most of the open access land area in California that is predicted to have increased suitability for *I. pacificus* in the coming decades is federally-owned, including areas like national forests and national parks. By the end of the century, 26% of all federal land in the state is predicted to be suitable habitat for *I. pacificus* under current land ownership (Table 3). Because the federal government manages almost half of the land area in California (178,000

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km^2), this represents a substantial land area (>45,000 km^2). Up to 29% of state-managed lands are expected to be suitable habitat, but since the state only owns 11,880 km^2 (3%) of land in California, this only represents about 3,471 km^2. And although 33% of the 6,554 km^2 (26.3%) of California lands managed by cities, special districts, non-profit organizations, and counties manage is expected to be suitable habitat, this still represents a substantially smaller land area than the federally-managed lands that will be suitable for *I. pacificus*.

4. Discussion

We previously estimated that 17% of California is suitable habitat for *I. pacificus* based on contemporary climate and land use information. Here, we predict a 23 to 86% increase in land area suitable for this vector under future climate change scenarios. By the end of the century, our models show that almost a third of California could be suitable *I. pacificus* habitat. Our models show a relatively small amount of habitat contraction, mostly in southern California, a region with high model uncertainty because future climate variables are projected to be outside of the historical range on which the model was built.

This pattern of habitat expansion contrasts with a recent model for *I. pacificus* in the western U.S. that was developed using tick presence records from citizen science submissions (Porter et al., 2021). Their future predictions show more continuous habitat in north central California and along the coast compared to results presented here, but overall, their models show a reduction in tick habitat compared to the present-day. One potential reason for disagreement in these projections is that the location information for tick occurrence records in Porter et al. (2021) was reported by community members, which may have resulted in misclassification (Eisen and Eisen, 2021). The major climate drivers in the Porter et al. (2021) future climate niche model were isothermality (33.6% contribution) and temperature seasonality (45.5% contribution). Although isothermality was selected as a variable in our contemporary ecological niche model for *I. pacificus,* it contributed 10% or less to explaining variation in our models (Eisen et al., 2018). While we used an ensemble modeling approach to assess model concordance for habitat suitability predictions, Porter et al. (2021) relied only on maximum entropy modeling for their assessment. Additionally, their models included tick presence points in Washington and Oregon, which may have influenced variable selection. Finally, their present-day habitat suitability maps include agricultural areas in the northern section of California’s central valley that were restricted in our analysis, which likely accounts for some of the differences in predicted suitability in this region. These discrepancies demonstrate the sensitivity of future habitat predictions to data inputs and methodology.

Most of the predicted habitat expansion from our models occurs in Northwestern and central coastal California where mean temperature and precipitation, both during the coldest quarter, are the major drivers, respectively. The winter months in California are the host-seeking period for adult I. pacificus in this region (Clover and Lane, 1995; Eisen et al., 2004; Kramer and Beesley, 1993; Lane and Stubbs, 1990; MacDonald and Briggs, 2016; Padgett and Lane, 2001; Salkeld et al., 2014). Others have shown that seasonal adult I. pacificus host-seeking activity was strongly and positively associated with monthly precipitation and minimum

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winter temperatures, and to a lesser extent was associated with winter precipitation (optimal between 100–300 mm) and vegetation. It is likely that future habitat suitability for I. pacificus will depend in part on the ability for adult ticks to survive when they are off-host.

Over a third of the future suitable tick habitat predicted by our models is classified as open access land (i.e. publicly available) across all scenarios and time periods, and the amount of open access land that is forecast to be suitable tick habitat doubles by the end of the century. This is notable because approximately one third of Californians who acquire Lyme disease have been exposed out of their county of residence, and it is recognized that time spent in recreational parks and open lands is a risk factor in exposure to ticks in California (Eisen et al., 2006, Salkeld *et al.*, 2019), in contrast to other regions of the country where people are more likely to be exposed to blacklegged ticks peridomestically (Connally et al., 2009). Future population projections for the state vary dramatically depending on the global scenario (or "Shared Socioeconomic Pathway, or SSP) (Hauer, 2019). For example, under the SSP3, or the "Regional Rivalry" pathway, there is an overall population decline in California and across the U.S. due to a strong governmental focus on regional security and decreases in immigration and investments in health and education (Hauer, 2019; Rohat et al., 2020). In contrast, SSP5, or the "Fossil-fueled Development" pathway, depicts high population growth in the U.S. driven primarily by immigration, along with investments in technology and human and social capital (Hauer, 2019; Rohat et al., 2020). The SSP5 projections show the most population growth in the Bay area, Sacramento region, the central and southern coast, and southern California (Hauer, 2019). Pairing the human population growth scenario (SSP5) with our future habitat suitability map, we might expect that human exposure to *I. pacificus* vectors would increase most substantially along the central and southern coast of California, particularly by the end of the century. It is important to note this may not translate directly to the risk of acquiring a tick-borne pathogen. State-wide prevalence of *Borrelia burgdorferi* sensu lato (sl), including the bacteria that cause Lyme disease, is about 0.6% in questing *I. pacificus* adults and 3.2% in questing *I. pacificus* nymphs (Padgett et al., 2014). Others have found wide variation in pathogen prevalence across tick sampling sites (Salkeld et al., 2021) with almost no risk of *Borrelia burdorferi* exposure in southern California (Rose et al., 2019). The density of infected host-seeking nymphal ticks, a primary determinant of human tick-borne disease risk, is determined in part by the presence of reservoir hosts capable of infecting ticks with disease agents (Eisen et al., 2010). We did not model *I. pacificus* hosts in this study, but we review the current knowledge about the future distribution of these species below.

Another strategy to model future Lyme disease risk is the approach used by Couper et al., 2021Couper *et al.*, which is to measure statistical associations between climate variables and Lyme disease incidence, without considering the distribution of tick vectors. In this coarse statistical approach, they found statistically insignificant changes in Lyme disease incidence for the majority of California. The authors cautioned that the Pacific Southwest model had low accuracy, perhaps due to being in a non-endemic region for Lyme disease. Similar to the present study, this statistical approach only considered part of the tick-borne disease system. Estimating the future risk of acquiring a tick-borne disease requires accurate assessments of the vector distribution, host distribution, and human behavior.

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Finally, our demonstrate show that almost all of the suitable habitat on open access lands is federally managed. A similar percentage of the state and city owned lands will also be suitable habitat, but this represents a much smaller land area. Public lands in California have their origins in 19th century laws that started with statehood in 1850 and continued through the century. The largest share of public lands in California are managed by four agencies: Bureau of Land Management (BLM), Fish and Wildlife Service (FWS), National Park Service (NPS) and Forest Service (FS). These lands are managed for many purposes, including recreation, conservation, and development of natural resources. The footprint of these lands is relatively stable: during the 19th century, laws encouraged western settlement through federal land disposal, but in the 20th century, emphasis has shifted to retention of federal lands (Congressional Research Service, 2020). Our finding points to the potential role of federal agencies that manage open access lands (e.g. national forests, national monuments and recreation areas, and national parks) in implementing tick and tick-borne disease management. This could be accomplished through collaboration between the BLM, FWS, NPS, and FS with the U.S. Centers for Disease Control and Prevention to design cost-effective management strategies that have been used in other parts of the U.S. For example, a modeling study in the Northeastern U.S., where the majority of U.S. Lyme disease cases occur (Nelson et al., 2015), found that awareness-based interventions, including distribution of signage, fliers, and presentations, was cost-effective and had the largest impact on lower Lyme disease risk compared to strategies targeting animal reservoirs (Behler et al., 2020). Other strategies could include landscape management or application of acaricides in high use areas near visitor centers to decrease human exposure to ticks (Stafford et al., 2017).

This study has a number of limitations. Because we were interested in the impact of future climate on the change in suitable *I. pacificus* habitat, both our contemporary and future ecological niche models only included climatic predictors. In our contemporary model, we restricted our results to forest, grass, scrub-shrub, and riparian areas using a land cover mask to exclude intensive agriculture areas, impervious surface, and aquatic areas that are unsuitable for *I. pacificus* survival (Eisen et al., 2004; Eisen et al., 2018; Furman and Loomis, 1984; Kramer and Beesley, 1993; Lane and Stubbs, 1990). We applied the same present-day land cover mask to our future projection of *I. pacificus* habitat in California. This methodology allowed us to isolate the direct effects of change in climate predictors on future *I. pacificus* habitat suitability; however, future changes in California land cover may further restrict or expand available vector habitat in ways that are not captured in our analysis. For example, an analysis of land cover change in California during the last decades of the twentieth century showed that developed lands increased by nearly 40% over this period, and the largest declines in land cover area were in the grass/shrublands and forest classes (Sleeter et al., 2011). If this trend continues, it would have a substantial impact on available habitat for *I. pacificus* in the state. Additionally, wildfire is a major land cover disturbance in the western U.S., and we are just beginning to understand the implications of these events on the ecology of tick-borne diseases (MacDonald et al., 2018; Pascoe et al., 2020).

Projecting future Lyme disease exposure risk should also consider potential shifts in range for the primary vertebrate hosts of *I. pacificus* in response to climate change, which will likely affect tick distribution and the prevalence of pathogens in the tick population. In

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California, the main hosts for adult *I. pacificus* include two subspecies of mule deer, Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and California mule deer (*O. h. californicus*), and several species of medium-sized mammals (Furman and Loomis, 1984). Immature ticks (larvae and nymphs) parasitize smaller vertebrates, particularly lizards, such as the western fence lizard (*Sceloporus occidentalis*) and alligator lizards (*Elgaria* spp.), as well as rodents (e.g., dusky-footed woodrat, *Neotoma* spp.; western gray squirrel, *Sciurus griseus*) and certain species of ground-foraging birds. There are no empirical studies of the responses of deer to climate change in California. However, a recent 21st century resurvey of small mammals and birds along a 3000-m elevational transect that initially were surveyed during the early 20th century, revealed some species-specific responses to climate change. For instance, some rodents (e.g., *Peromyscus truei*) had expanded their ranges from lower to upper elevations, whereas other species (*P. boylii, P. maniculatus)* did not make any niche adjustments (Moritz et al., 2008). Many bird species evinced a range shift by moving toward wetter or cooler conditions commensurate with their preferred niches (Tingley et al., 2009).

More recently, ecological niche models were developed for all 153 reptilian and amphibian species known to occur in California to forecast the distribution of climatically suitable habitat for 2050 under four future climate scenarios and 11 general circulation models (Wright et al., 2013). The western fence lizard, the principal maintenance host for *I. pacificus* immatures in many biotopes throughout the state (Jellison, 1934; Lane and Loye, 1989), fell into a broad category comprising about 60–75% of the reptilian and amphibian species that were predicted to experience less than 20% loss of suitable habitat. Contrarily, 12% of 200 Mexican sites in which 48 species of *Sceloporus* lizards had been surveyed between 1975 and 1995 were locally extinct by 2009 when resurveyed from 2006 to 2008 (Sinervo et al., 2018). As we continue through the 21st century, the changing climate will likely impact tick-borne disease ecology in myriad ways, including through impacts on the assemblages of tick hosts.

In conclusion, using contemporary climate-based habitat suitability models and climate change projections in California, we developed future habitat suitability projections for *I. pacificus*, a vector of medical importance. By overlaying open access boundaries and land ownership, we identified the agencies that will most likely need to integrate tick management or public outreach about ticks and tick-borne diseases into future planning processes. Ongoing tick surveillance in areas of predicted expansion in tick habitat will be important for assessing the changing risk of human Lyme disease in the state.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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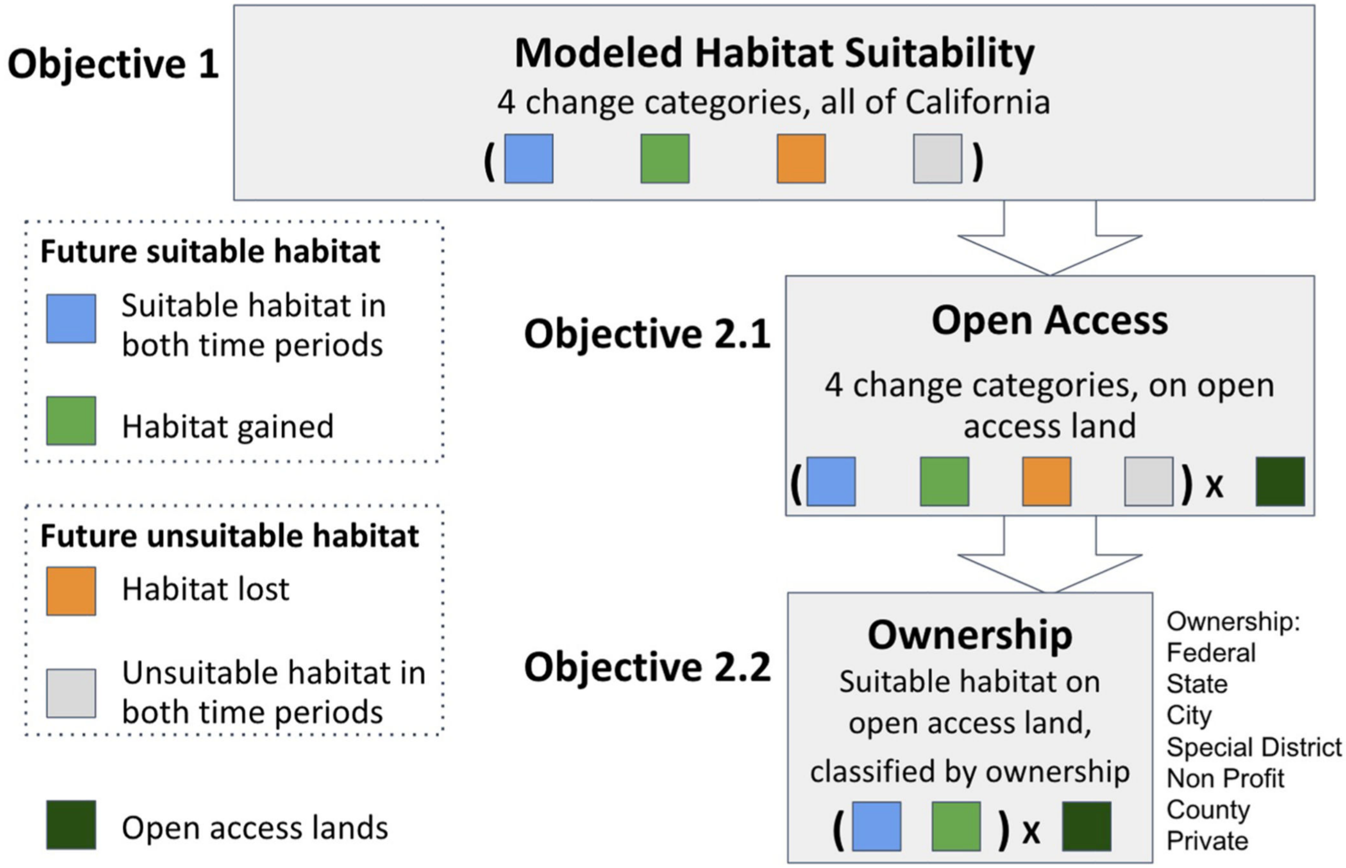

Figure 1.
Workflow for investigating access and ownership of the land predicted to be suitable *I. pacificus* habitat under future climate scenarios.

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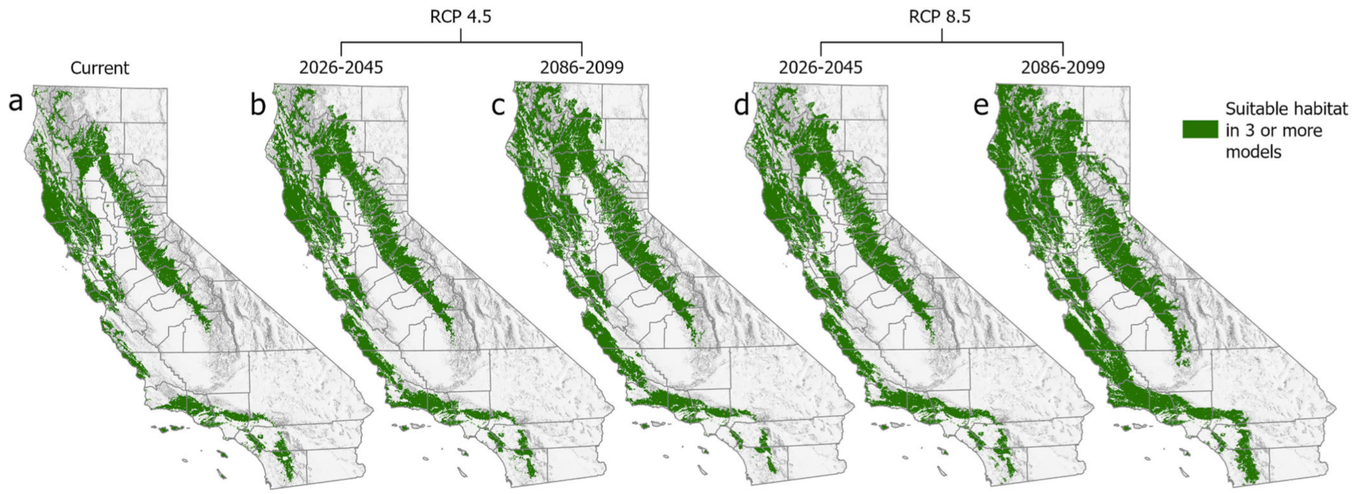

Figure 2.

Maps displaying consensus of three or more models predicting habitat suitability for in the present day and future time periods under two climate scenarios a) current, b) mid-century RCP4.5; c) end-of-century RCP4.5; e) mid-century RCP8.5; and e) end-of-century RCP8.5. All models used ensemble means climate model. Scores indicate the number of the five optimized models that predict habitat suitable for the establishment of *I. pacificus*.

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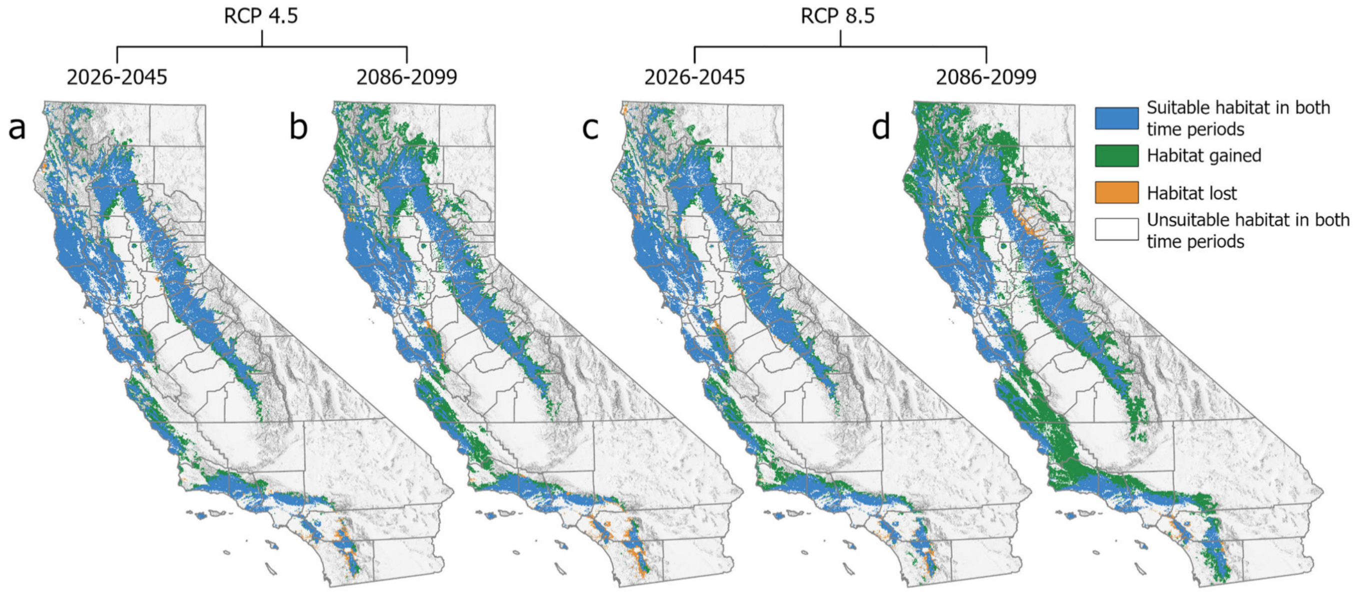

Figure 3.

Predicted change from present-day *I. pacificus* habitat suitability under four climate scenarios: a) mid-century RCP4.5; b) end-of-century RCP4.5; c) mid-century RCP8.5; and d) end-of-century RCP8.5. All models use an ensemble means climate model.

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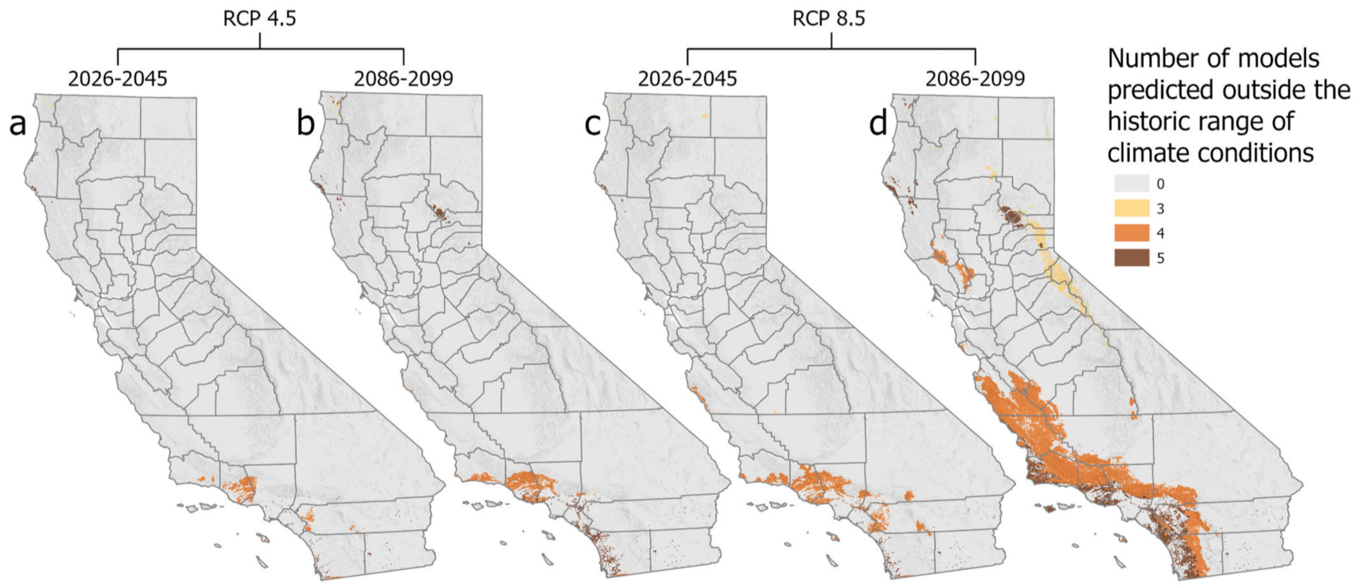

Figure 4.

Multivariate Environmental Similarity Surface (MESS) ensemble maps: a) mid-century RCP4.5; b) end-of-century RCP4.5; c) mid-century RCP8.5; and d) end-of-century RCP8.5. All models use an ensemble means climate model within a GLM statistical framework. The threshold value that achieved 90% sensitivity in the model output was used to transform the continuous probability output to a binary indicator of habitat suitability.

Table 1

Modeled change in land area suitable for *Ixodes pacificus* under four climate scenarios for California

Change category	RCP4.5 (2026–2049) (km^2)	% of CA	RCP4.5 (2086–2099) (km^2)	% of CA	RCP8.5 (2026–2049) (km^2)	% of CA	RCP8.5 (2086–2099) (km^2)	% of CA
Future suitable habitat	**88,333**	**21.6**	**100,568**	**24.6**	**92,306**	**22.5**	**132,941**	**32.5**
Suitable in both time periods	69,036	16.9	68,307	16.7	69,223	16.9	69,219	16.9
Habitat gained	19,297	4.7	32,260	7.9	23,083	5.6	63,723	15.6
Future unsuitable habitat	**321,109**	**78.4**	**308,875**	**75.4**	**317,136**	**77.5**	**276,501**	**67.5**
Habitat lost	2,089	0.5	2,818	0.7	1,902	0.5	1,907	0.5
Unsuitable in both time periods	319,020	77.9	306,057	74.7	315,234	77	274,594	67.1

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Table 2

Modeled change in open access land area suitable for *Ixodes pacificus* under four climate scenarios for California

Change category	RCP4.5 (2026–2049) (km^2)	% of CA	RCP4.5 (2086–2099) (km^2)	% of CA	RCP8.5 (2026–2049) (km^2)	% of CA	RCP8.5 (2086–2099) (km^2)	% of CA
Future suitable habitat	**31,363**	**7.7**	**33,521**	**8.2**	**36,640**	**8.9**	**51,522**	**12.6**
Suitable in both time periods	23,363	5.7	23,440	5.7	22,869	5.6	23,100	5.6
Habitat gained	8,000	2	10,082	2.5	13,771	3.4	28,422	6.9
Future unsuitable habitat	**162,399**	**39.7**	**160,241**	**39.1**	**157,122**	**38.4**	**142,240**	**34.7**
Habitat lost	624	0.2	548	0.1	1,118	0.3	888	0.2
Unsuitable in both time periods	161,775	39.5	159,93	39	156,003	38.1	141,353	34.5

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Table 3

Modeled change in open access land area by ownership status suitable for *Ixodes pacificus* under four climate scenarios for California

Ownership	**RCP4.5 (2026–2049) (km^2)**	**% of CA**	**RCP4.5 (2086–2099) (km^2)**	**% of CA**	**RCP8.5 (2026–2049) (km^2)**	**% of CA**	**RCP8.5 (2086–2099) (km^2)**	**% of CA**
Federal	26,734	6.5	31,921	7.8	28,884	7.1	45,877	11.2
State	2,860	0.7	2,931	0.7	2,803	0.7	3,471	0.9
County, Special District, City, Non Profit, and Private	1,769	0.4	1,788	0.4	1,835	0.5	2,174	0.5