



The importance of geography in forecasting future fire patterns under climate change

Alexandra D. Syphard^{a,1} , Santiago José Elías Velazco^{b,c} , Miranda Brooke Rose^d , Janet Franklin^e , and Helen M. Regan^f 

Edited by Glen MacDonald, University of California, Los Angeles, CA; received June 22, 2023; accepted December 7, 2023

An increasing amount of California's landscape has burned in wildfires in recent decades, in conjunction with increasing temperatures and vapor pressure deficit due to climate change. As the wildland–urban interface expands, more people are exposed to and harmed by these extensive wildfires, which are also eroding the resilience of terrestrial ecosystems. With future wildfire activity expected to increase, there is an urgent demand for solutions that sustain healthy ecosystems and wildfire-resilient human communities. Those who manage disaster response, landscapes, and biodiversity rely on mapped projections of how fire activity may respond to climate change and other human factors. California wildfire is complex, however, and climate–fire relationships vary across the state. Given known geographical variability in drivers of fire activity, we asked whether the geographical extent of fire models used to create these projections may alter the interpretation of predictions. We compared models of fire occurrence spanning the entire state of California to models developed for individual ecoregions and then projected end-of-century future fire patterns under climate change scenarios. We trained a Maximum Entropy model with fire records and hydroclimatological variables from recent decades (1981 to 2010) as well as topographic and human infrastructure predictors. Results showed substantial variation in predictors of fire probability and mapped future projections of fire depending upon geographical extents of model boundaries. Only the ecoregion models, accounting for the unique patterns of vegetation, climate, and human infrastructure, projected an increase in fire in most forested regions of the state, congruent with predictions from other studies.

fire regime | climate change | California | fire distribution model | ecoregion

California has long been associated with wildfires and the devastating human impacts that wildfires can cause. For example, the Bel Air Fire of 1961 and the Oakland Hills fire in 1991 had such an impact that they are still discussed today (1–3). In recent years, California wildfire has become even more prominent in the media and the scientific literature, as the state has experienced a record-breaking number of large fires (4), many of which have resulted in unprecedented loss of life and property (5), leaving many communities to deal with complex and long-lasting delays in recovery (6). Dramatic changes in the frequency, severity, and timing of wildfires are also driving large-scale ecosystem changes that exceed the resilience of many native species (7–9). Although California may have the most high-profile destructive fires, record-breaking fire seasons and enormous wildfire impacts to human communities are happening globally. Lessons learned in California will set examples for the rest of the world. While there are multiple reasons for recent increases in wildfire activity, climate change has been largely implicated for its effects on fuel aridity and longer fire seasons, and there is broad concern that climate change will further increase fire risk in the future (10, 11). Land use change and increases in the wildland–urban interface will further increase human exposure to wildfire and exacerbate existing social vulnerabilities (12, 13). Given these serious consequences and dire predictions, there are strong calls and hefty financial resources for action to increase social and ecological resilience to wildfire (e.g., ref. 14). Creating a fire-resilient future where people coexist with wildfire will require implementing multiple strategies coordinated through diverse stakeholders that are tailored to specific social and biophysical conditions and objectives (15–17). The question, then, is what is needed where, when, and why?

The answer to this question is particularly complicated in California because the state has a wide diversity of natural fire regimes, i.e., the long-term characteristics of wildfire (e.g., size, severity, frequency, and seasonality) within a given ecosystem (18, 19). Variation in fire regimes manifests in response to the distinctive combinations of ignition patterns, vegetation characteristics, climatic and atmospheric conditions, and topography that characterize a given region over time, as these are the factors that dictate the timing, location, and behavior of recurrent wildfires (20). In turn, fire regimes exert strong controls over ecosystem functioning and structure, and they are prominent drivers of species' evolution

Significance

Models and maps anticipating how fire patterns may change in response to climate change and other drivers are important tools for climate-resilient protection of ecosystems and human communities. When using these models for decision-making, however, it is critical to understand their sources of uncertainty. We show that different geographical extents of model boundaries can result in nearly opposite future fire predictions for the same geographical areas—illustrating geographical variation in both fire regimes and their predictability. There is no one-size-fits-all prediction for fire futures in California or a single strategy to mitigate fire risk to people, infrastructure, and ecosystem resilience. Modeling and decision-making may be most reliable if constrained to the geographical limits of specific fire regimes.

Author contributions: A.D.S., S.J.E.V., J.F., and H.M.R. designed research; S.J.E.V. and M.B.R. performed research; A.D.S. and M.B.R. analyzed data; and A.D.S., S.J.E.V., M.B.R., J.F., and H.M.R. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2024 the Author(s). Published by PNAS. This open access article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

Although PNAS asks authors to adhere to United Nations naming conventions for maps (<https://www.un.org/geospatial/mapsgeo>), our policy is to publish maps as provided by the authors.

¹To whom correspondence may be addressed. Email: asyphard@consbio.org.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2310076121/-/DCSupplemental>.

Published July 29, 2024.

(21) and community assembly (22). Given the long historical links between fire and species' traits and persistence (23), it is important to understand how altered fire regimes can greatly disrupt ecosystem structure and function, to the point that ecosystems transform into different states (24).

Fire regimes have been altered in multiple ways for various reasons. In addition to climate effects on wildfire in recent years, nearly a century of effective fire suppression in historically frequent-fire forests has led to substantial fuel accumulation and, consequently, a recent increase in large, uncharacteristically severe fires (25). On the other hand, increased human-caused fire ignitions resulting from population growth and urban expansion have substantially increased fire frequency in the shrublands that extend across the coastal and foothill regions of the state—areas where lightning is rare and where fire was historically infrequent (26, 27). Coupled with the increase in fire frequency, the expansion of Eurasian annual grasslands further promotes fire ignitions and threatens to cause massive vegetation change (8, 28). In previous centuries, California's fire regimes were altered by Euro-American settlement and associated processes of land use and management (grazing and changes in herbivore assemblages, logging, mining, and fire suppression) (29) and removing Indigenous people and their cultural burning and other stewardship practices from the land (30–32). Legacies of these changes are reflected in the vegetation across the state today. In short, there is tremendous geographical variability not only in natural fire regimes but also in how different drivers, such as climate change, vegetation management, land use change, invasive species, and unsustainable natural resource use are affecting them. Unraveling these effects is an ongoing priority in scientific research (33) and for ecological management.

While the complex drivers of altered fire regimes need further investigation, one of the most important tools that managers and decision-makers need now for prioritization and resource allocation are maps that help them anticipate where fires are most likely to occur, now and in the future. To meet this demand, a rapidly growing number of researchers and practitioners are developing methods and models to produce maps reflecting the geographical distribution of where current and projected future fire activity are likely to occur (hereafter fire distribution maps; FDM). FDM are being used for a variety of purposes. For example, the US Fish & Wildlife Service is using maps of future fire potential to guide the location of vegetation management treatments to protect carnivore species of concern (34). The state of California uses future fire projections for informing resilience actions (35). Future fire projections have also been used to estimate wildfire risk to electricity transmission lines (36).

Several fire mapping and modeling approaches have been developed, such as the dynamic simulation and overlay of individual fire behavior maps (37). However, the most common approach is to use statistical or machine learning methods (38), as in species distribution modeling (39), such that historical observations of wildfires are associated with predictor variables reflecting the environmental conditions that control where wildfires occur. The models are then projected onto continuous maps of the explanatory variables, typically including future projections of the climate variables used as model predictors when forecasting climate change effects on fire regime. One limitation of this approach is that the models assume the nature of fire–climate relationships will persist into the future, whereas both the relationships and the climate may present “no-analog” conditions (40).

Fire distribution maps have been produced at varying geographical extents, from landscape to continental (e.g., refs. 41 and 42), to map fire properties such as ignition locations (43), fire occurrence (44),

locations of large fires (45), or fire severity (46). As with species distribution models, there have also been analyses of the sensitivity of model parameters and performance to predictor variable type and selection (e.g., ref. 47) or modeling method and algorithm (e.g., ref. 48). The geographical extent at which fire distribution models are trained and mapped is of particular interest for a state like California in which relationships between wildfire patterns and their drivers, e.g., climate–fire or human–fire relationships, are nonstationary (e.g., ref. 49). Thus, it is reasonable to assume that the direction and strength of relationships modeled in one region may not apply to other regions. Often, fire distribution maps and models are trained at large geographical extents with subsequent finer-scale analyses focusing on specific localities (e.g., refs. 35 and 46). However, given the known spatial variation between fire patterns and drivers, and the importance of these maps for decision-making, an important question is whether the treatment of geography in these models makes a difference in outcomes for both baseline and future projected conditions—particularly projections that are important for climate change adaptation.

Although the effect of geographical modeling extent on baseline and future fire projections has not been systematically evaluated, Syphard et al. (50) found that the relative importance of different explanatory variables and the nature of the relationships varied for distribution models of fire occurrence and large fires for three different regions in California. In addition, Park et al. (51) performed an experiment in which they compared the performance of models trained within smaller-scale subregions throughout California with the performance of models trained statewide, and they found that the broader-scale model produced higher model performance. However, they did not evaluate differences in variable importance or in future fire occurrence projections under climate change. In this paper, we take this line of inquiry further and compare model results and mapped output from models developed to predict the probability of occurrence of fires ≥ 40 ha in size 1) across the entire state, 2) across the entire state using ecoregions as a predictor variable, and 3) across 10 separate ecoregions in California. In addition to comparing results for a baseline time frame (1981 to 2010), we use our models to project future patterns of change under climate change scenarios.

We specifically asked

- 1) How do model accuracy, variable importance, and mapped projections vary depending on geographical extent of analysis?
- 2) Does the addition of ecoregion as a predictor variable in a statewide analysis yield similar results as the development of separate models trained for each ecoregion?
- 3) Are divergences in treatment of geographical extent exacerbated in future projections?

Results

Fire Distribution Model Performance. Fire distribution models (FDM) were trained using 3,902 fires occurring between 1981 and 2010 (baseline), predicted from climate, terrain, and land use variables, and modeled using the Maxent algorithm, for the state of California (with and without ecoregion as a predictor), and separately for 10 ecoregions (*Materials and Methods*). When produced for all fire occurrence data statewide, models performed similarly well, regardless of including ecoregion as a predictor variable (Table 1). Interestingly, including ecoregion as a predictor variable in the statewide FDM led to an increase in true positive rate and a subsequent decrease in true negative rate (greater commission error—predicting fire where it did not occur).

Table 1. Six performance measures of fire distribution models produced for California and within ecoregions (ranges given for 10 ecoregions)

Performance metric	California-wide		Ecoregion-specific (range of means)
	Without ecoregion	With ecoregion	
AUC	0.80 ± 0.01	0.80 ± 0.02	0.56 (±0.05) to 0.93 (±0.05)
TSS	0.45 ± 0.02	0.45 ± 0.02	0.22 (±0.06) to 0.082 (±0.07)
True positive rate	0.74 ± 0.05	0.82 ± 0.12	0.65 (±0.19) to 0.95 (±0.04)
True negative rate	0.71 ± 0.04	0.63 ± 0.11	0.46 (±0.27) to 0.88 (±0.06)
Sorensen index	0.73 ± 0.02	0.74 ± 0.03	0.47 (±0.19) to 0.89 (±0.05)
Inverse mean absolute error	0.64 ± 0.007	0.65 ± 0.009	0.51 (±0.01) to 0.90 (±0.01)

AUC, area under the curve (of the receiver-operator characteristic plot); TSS, true skill statistic (*Materials and Methods*).

For the ecoregion-specific models, performance varied considerably (Table 1). Across most performance metrics, the model constructed solely for the Modoc Plateau ecoregion performed the worst, likely due to the low true negative rate observed for this ecoregion (*SI Appendix, Table S1*). Ecoregion models that performed better than the statewide models in at least one performance metric included those for the largely nonforested Mojave Desert, the Sonoran Desert, Great Valley, and Southwestern ecoregions (*SI Appendix, Table S1*).

Differences in Spatial Predictions for Baseline Time Period (1980 to 2010). Differences in the geographical predictions made by the three FDM approaches for the baseline (1980 to 2010) time period were spatially structured (Fig. 1). These differences were greatest in the Modoc Plateau, east of the Sierra Nevada, and along the western edge of the Sonoran and Mojave Desert ecoregions where they border Southwestern California (refer to Fig. 2C for ecoregions). The two statewide FDM showed broadly similar geographical patterns of predicted fire probability (Fig. 1D), except in the region East of the Sierra Nevada, where including ecoregion as a predictor led to reduced predicted fire probability, better representing the observed, low fire activity in this region than the other models (Fig. 1G–I). While both statewide FDM predicted similar levels of fire probability in the Modoc Plateau, the local model constructed for this ecoregion predicted much higher fire probability, leading to overprediction that was evident when comparing the mapped output to observed fires (Fig. 1I). Compared to the statewide models, the ecoregion-specific models also predicted slightly higher fire probability across the Mojave Desert and Cascade Ranges; slightly lower fire probability across the Southwestern and Sonoran Desert, and a mix of differences in the Northwestern, Central Valley, Great Valley, and Sierra Nevada.

Environmental Predictors of Fire Probability. Topographic heterogeneity and temperature seasonality were the most important predictors of fire occurrence in both statewide models (Fig. 2 and *SI Appendix, Figs. S1 and S2*). Ecoregion ranked third in variable importance when it was included, while climatic water deficit ranked third when ecoregion was not included. Variables related to anthropogenic factors, including distance to urban areas or roads and urban density, were less important than terrain and climate in the statewide models. However, variable importance and response curves (i.e., the nature of the relationship based on partial dependence plots) varied greatly among ecoregion-specific FDM (*SI Appendix, Figs. S3–S12*). Although distance to principal roads was the least important variable in the statewide models, it ranked as the most important in the ecoregion East of the Sierra Nevada, where it had a negative relationship with fire probability (*SI Appendix, Fig. S11*). Similarly, housing density

was an important ecoregion-specific factor for predicting fire probability in Southwestern California, where fires were least likely to occur in areas with high housing density (*SI Appendix, Fig. S12*). Topographic heterogeneity was the most important predictor of, and positively related to, fire probability in the Cascade Ranges, Great Valley, Modoc Plateau, Northwestern, and Southwestern ecoregions (*SI Appendix, Figs. S4, S7–S9, and S12*). Temperature seasonality was most important, and inversely related to fire probability, in the arid, continental Mojave and Sonoran Deserts (*SI Appendix, Figs. S5 and S6*), while it was most important but positively related to fire in the Sierra Nevada and Central Western California (within those ecoregions, locations with greater temperature seasonality had more fire; *SI Appendix, Figs. S4 and S10*).

Projections of Fire Probability under Climate Change. Projections of future fire probability under climate change were highly dependent on model building technique (*SI Appendix, Fig. S13*). Specifically, local models built for each ecoregion often differed substantially from the statewide FDM in both the amount of fire predicted and the projected trend under climate change scenarios. These differences were most readily observed when comparing the projected change in fire probability through time (Fig. 3 and *SI Appendix, Figs. S14 and S15*). For example, while the statewide FDM predict a decline in fire probability across the forested Cascade Ranges, Northwestern, and Sierra Nevada ecoregions under future climate scenarios, the ecoregion-specific model predicts an increase in these areas. On the other hand, the ecoregion-specific model and statewide FDM with ecoregion as a predictor show similar fire probability trajectories in the Sonoran Desert, both predicting lower levels of fire probability than the FDM without ecoregion as a predictor. Overall, model-building technique was more important than climate change scenario in determining future fire probability across California. However, the statewide FDM without ecoregion as a predictor predicted greater decreases in fire probability under HadGEM2-ES RCP 8.5 in the Northwestern, Sierra Nevada, Great Valley, and Sonoran Desert ecoregions compared to the other climate change scenarios.

Discussion

Wildfire is one of the biggest challenges that the state of California faces in terms of both ecological and social sustainability. Altered fire regimes are leading to dramatic ecological transformations, and there are human communities still recovering from wildfires in 2018 and 2020; and yet, continued wildfire is inevitable. Building a fire-resilient future will require informed strategies that facilitate coexistence of humans and fire where fire is ecologically beneficial, while preventing excessive or destructive fires where

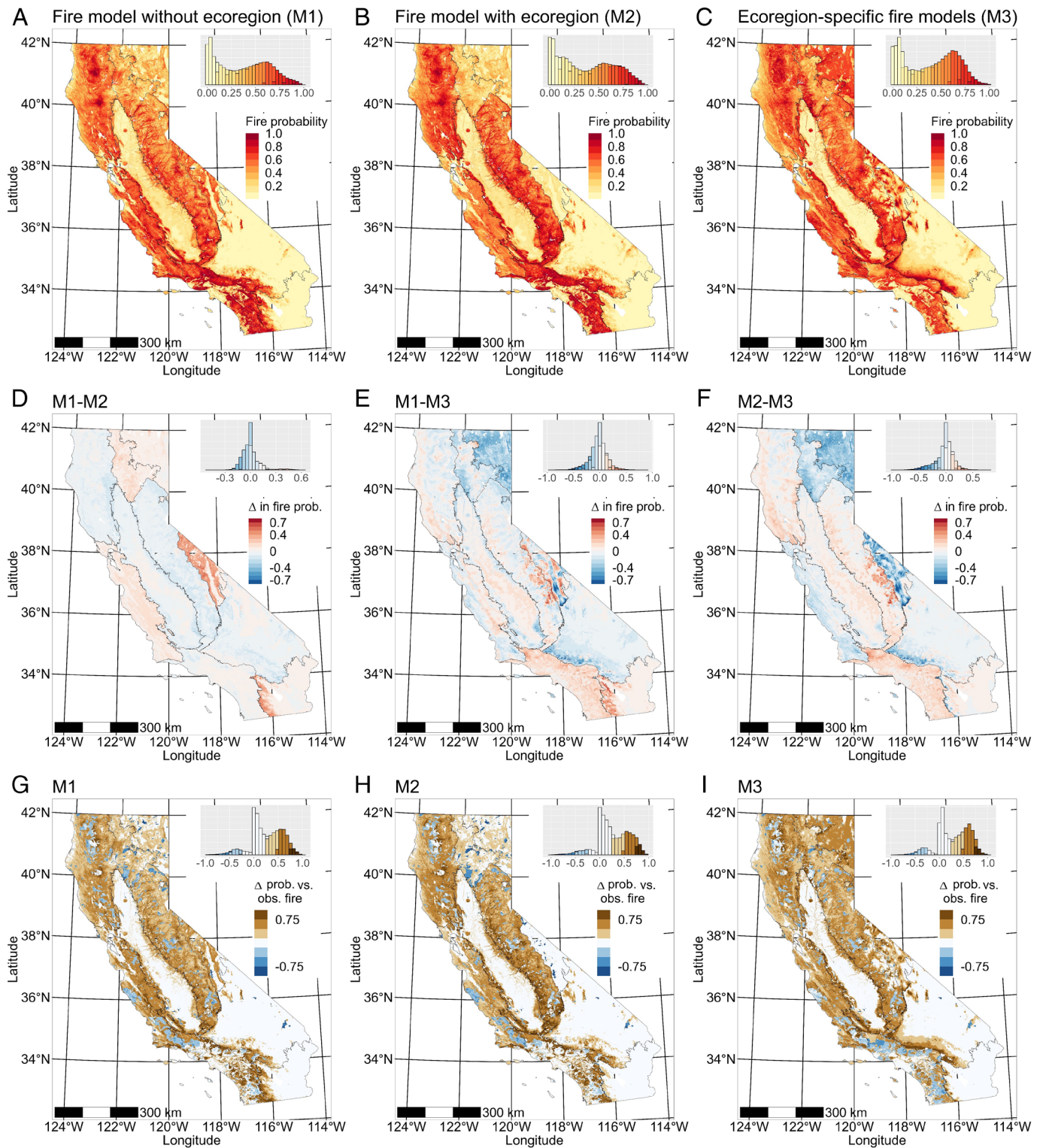


Fig. 1. Mapped fire probability and differences between predicted fire probability, and observed fire occurrence 1980 to 2010 for fires >40 ha. Fire probability predictions made by a statewide FDM without ecoregion as a predictor variable (M1) (A), a statewide FDM with ecoregion as a predictor variable (M2) (B), and a set of local models built for each ecoregion (M3) (C). Difference between mapped fire probabilities predicted by M1 and M2 (D), M1 and M3 (E), and M2 and M3 (F). Difference between mapped fire probabilities and fire polygons under baseline conditions for M1 (G), M2 (H), and M3 (I). In the bottom row, positive numbers indicate areas with predicted high fire probability but no fire occurrences during the study period (“overprediction”), while negative numbers correspond to areas where a fire(s) occurred, but the fire model predicted low fire probability (“underprediction”). In each panel, the histogram shows the frequency distribution of pixels for the values shown in that panel’s map.

humans are most at risk and fire frequency exceeds the ecological resilience of natural communities. The wildfire toolbox contains numerous possibilities, including vegetation management and prescription burning at different locations, spatial extents, and

timing intervals; ignition prevention programs; invasive species management; land use policy and building codes; climate adaptation; homeowner mitigation strategies; and fire suppression. Given the diverse changes in different fire regimes, the biggest

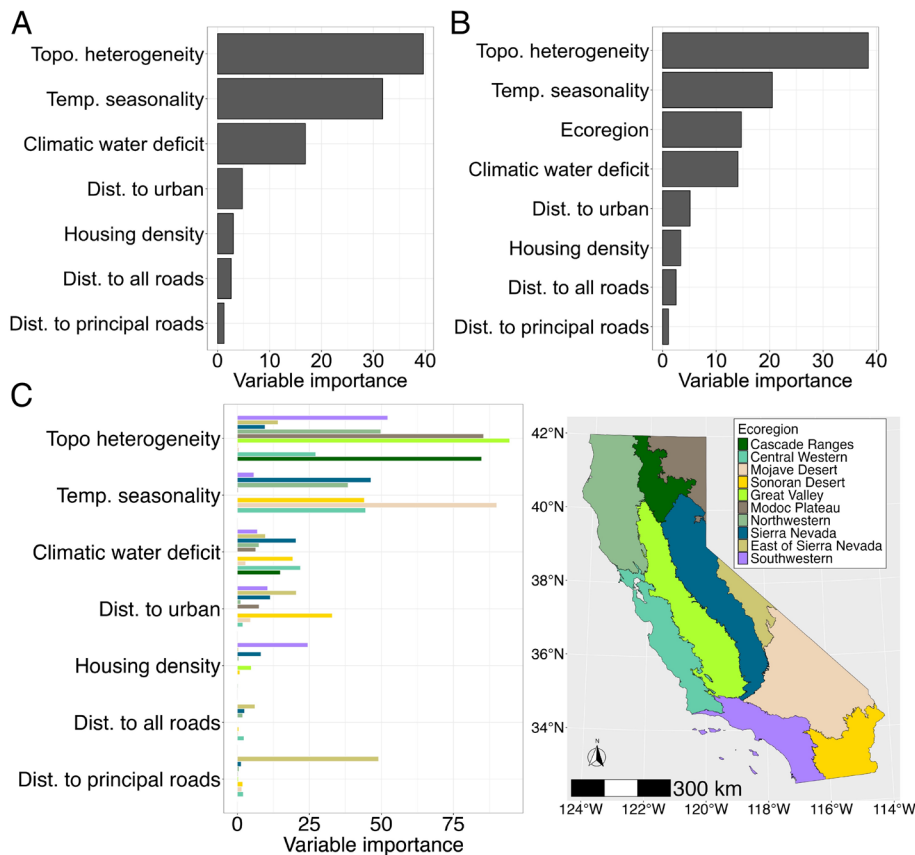


Fig. 2. Variable importance for (A) the two statewide fire distribution models without ecoregion as a predictor variable and (B) with ecoregion as a predictor, as well as (C) the variable importance within each ecoregion for the ecoregion-specific FDMs and a map of the ecoregions used in this study.

challenge for decision makers is to identify which strategies provide the most benefits where, and with the fewest costs. In all cases, maps showing where fire is most likely to occur now and in the future are an important tool for addressing this challenge. The key to their effectiveness is understanding their appropriate application in the face of model uncertainty.

In this study, in which we compared statewide fire distribution maps to maps produced separately for different ecoregions, we found that the geographical extent of analysis resulted in substantial variation in model accuracy, variable importance and direction of influence, and spatial prediction, especially when projecting fire under future climate conditions. On the other hand, using ecoregion as a predictor variable in the statewide model did not greatly affect model accuracy or output, although a higher commission error resulted in larger areas being mapped as suitable for fire in some ecoregions. These results have strong implications for the interpretation of mapped fire predictions.

At a statewide geographical extent, models produced with and without ecoregion as a predictor performed similarly (AUC 0.80). Park et al. (51) found similar model performance for an annual fire distribution model for California (AUC 0.77), which performed slightly better when developed statewide than it did for separate subregions (mean AUC 0.72), although individual AUCs were not provided. On the other hand, our model performance varied widely for the ecoregion-specific models, with some ecoregions having better model performance than the statewide model, and some worse.

Among the ecoregions in our study with the highest model performance, the desert ecoregions and Central Valley experience relatively low fire activity. However, they border the Southwestern region, which had high model performance and has the largest

amount of fire in the state (*SI Appendix, Table S2*). Therefore, the overall amount of fire in a region did not influence model performance, but there was an effect of ecoregion conditions. The higher-performing ecoregions are largely dominated by nonforested vegetation, and the primary driver of altered fire regimes has been an increase in fire frequency due to human-caused ignitions, and in some areas, the expansion of flammable invasive grasslands (29, 52–54). On the other hand, the lower-performing ecoregions farther north had higher proportions of forest, with many of these forests having experienced increased fuel accumulation and uncharacteristically large, severe fires in recent years due to legacies of fire suppression (55). Whereas human influence via population growth and land use change has been a strong driver of wildfire in coastal and lower-elevation shrublands, the higher-elevation conifer forests are the areas in the state where climate has exhibited a more direct influence on fire activity (49). These forests have also experienced massive tree mortality in response to drought and insect attack (56).

Although wildfire in California is driven by a combination of human, topographic, vegetation, and climatic variables, it is the differences in spatial and temporal patterns of these drivers (i.e., the fire regime) that most likely explains the variation between ecoregion and statewide models. Geographical differences were evident in the different rankings of variable importance and the variation in nature and direction of statistical response curves. This is consistent with another study using FDM in three California regions that reported regional differences in variable ranking and response curves (40). These results also reflect findings in empirical studies showing geographical variation in historical fire–climate relationships (57–59). Fire activity has also been shown to vary across aridity and productivity gradients (60–62).

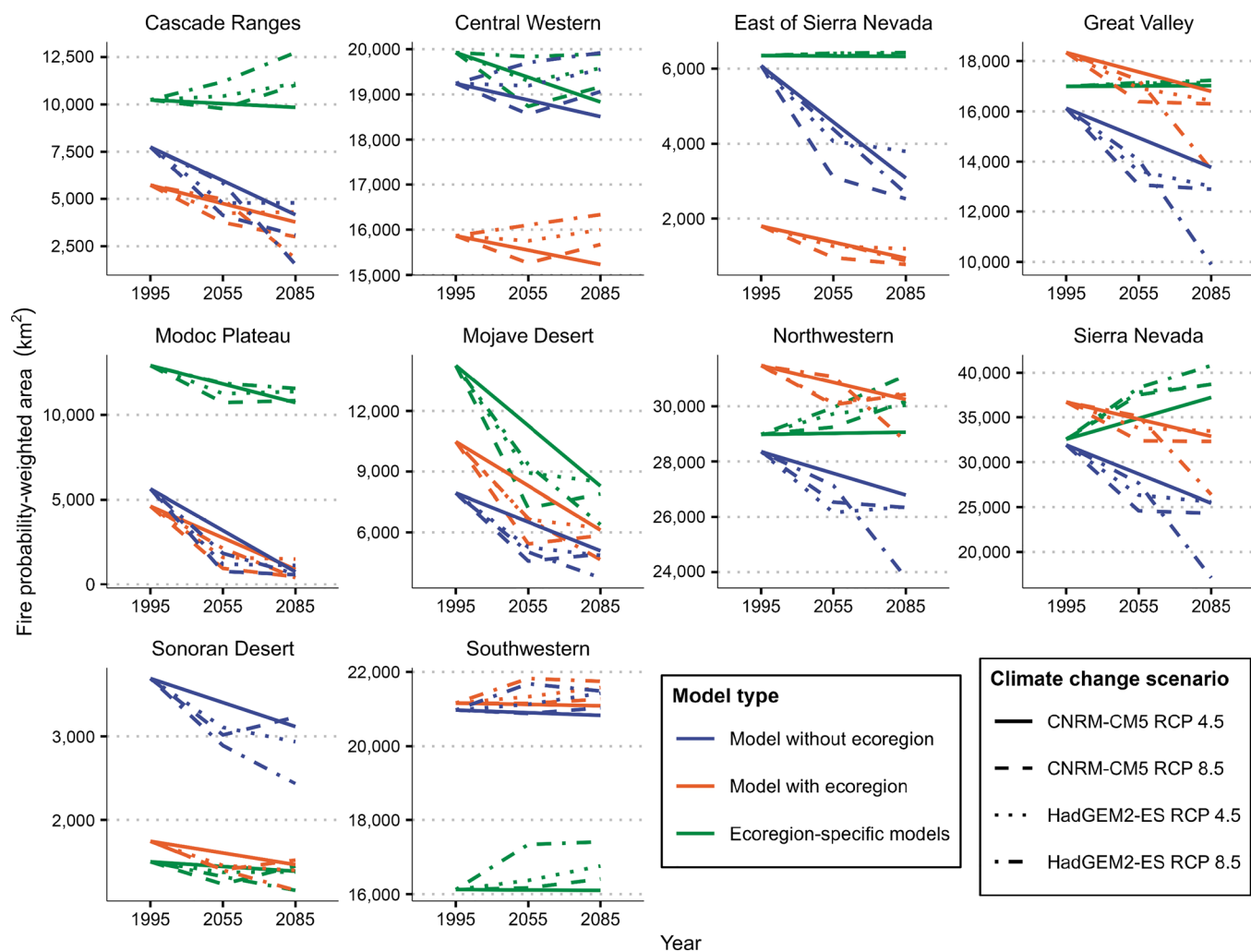


Fig. 3. Projected temporal trends in fire probability-weighted area across each ecoregion in California for the model types (color) and climate change scenarios (line type) explored in the current study. Note that the y-axis limits vary by ecoregion, to highlight the differences between model type and climate change scenario.

Local variation in fire–environment relationships may represent smaller segments of broad, nonlinear response curves that span a fuller range of environmental conditions, potentially contained within larger areas, like California (51). However, even given predictable responses of fire to broad gradients of fuel and moisture conditions, those fire–environment relationships are mediated locally by other unique characteristics of the region which comprise the fire regime. For example, human-caused ignitions corresponding to Santa Ana winds are responsible for many of the large, destructive wildfires in southern California (63), and those wind-driven fires have distinctive spatial patterns (64). The California-wide models of fire probability estimated in this study and others, therefore mix data from different fire regimes. In contrast, ecoregions, being defined based on vegetation mosaics, climate, and physiography, are reasonable approximations of regions that support a single fire regime (e.g., the historical Fire Regime Groups shown in refs. 25 and 52). An important consideration is that, despite the large amount of research on California wildfire, we still have an incomplete understanding of the environmental drivers of wildfire occurrence, particularly over different spatial and temporal scales.

While statewide models performed well for baseline conditions, they estimated fire response curves that mixed the effects of environment on fire from different fire regimes. Thus, models developed for ecoregions were generally better at reproducing expected relationships between environment and fire within a particular

fire regime. In some of the poorer-performing ecoregions, however, it is possible that we did not include the most relevant predictor variables.

For example, some of the poorer-performing, higher-elevation forested regions experience more lightning than other parts of the state (65), and have also been altered due to legacies of fire suppression (55), so it is possible that predictors delineating lightning strike potential, vegetation management, or fire history, might improve the performance of those models. It is also possible that some of our ecoregion boundaries did not accurately delineate distinctive fire regimes. Alternative methods exist for stratifying larger regions into smaller extents for modeling fire (e.g., refs. 19, 66, and 67).

Another important consideration is that our FDM projected fire occurrence as a function of long-term climate normals instead of shorter-term meteorological events that are more likely to influence fire behavior and interannual variability in wildfire activity. Whereas 30-y averages capture cumulative spatial differences in climatic variation, they do not account for extreme wind or weather conditions that often result in the most destructive wildfires (68) or in seasons with anomalously high fire activity (69). While our baseline models did not account for the years of high fire activity after 2010, many of the larger fires in recent years have occurred in the lower-performing ecoregions.

One of the most serious implications in choosing a geographical extent for FDM is illustrated in the large discrepancy in future

climate projections. Models built using fire occurrence data from all of California, with and without ecoregion as a predictor, predicted declining fire probability across the state under most climate change scenarios and in most ecoregions. On the other hand, most of the northern forested ecoregion-specific models projected increased or stable fire occurrence under climate change. The direction of projected change was most similar in the desert ecoregions.

In general, climate change is likely to have variable effects on future fire activity depending on the extent to which fire in a region is limited by vegetation amount (fuel volume) or vegetation moisture (fuel flammability) (70). With fire regimes as diverse as they are in California, it is counterintuitive and unlikely to expect climate to result in a net decline of fire across the entire state. Some research projected a net increase of fire in California due to climate change (47), and others projected climate-driven increases in area burned or fire frequency in northern and coastal forested regions with decreases in desert areas, which is generally similar to our ecoregion-specific results (71, 72). The probability of large fires was projected to increase under two climate scenarios in two northern California regions, with minimal effect of climate in southernmost San Diego County (50). FDM created for Mediterranean ecosystems worldwide also projected spatially heterogeneous responses of fire to climate change under a range of climate models (73). The authors suggested these differences may be owing to the nature of Mediterranean ecosystems that encompass divergences in fuel moisture versus fuel volume limitations to fire.

The downward trend in fire occurrence predicted by our statewide model is likely due to climate models predicting levels of temperature seasonality and climatic water deficit throughout many parts of California that are currently only observed in the arid desert regions, which tend to experience lower fire occurrence due to lower fuel volume. Because our models did not explicitly consider vegetation as a predictor variable, the statewide models erroneously predicted desert-like levels of future fire occurrence across much of California as temperature seasonality and climatic water deficit were forecast to increase to unprecedented levels (desert-like climate in places without a legacy of desert-like vegetation). In this sense, our statewide model differs from other statewide FDM that predicted stronger increases in wildfires, particularly in densely vegetated areas (e.g., refs. 35, 47, 71, and 72). This may be partly because the other models used different climate models (GCMs) or different combinations of climate variables. In some studies, a combination of actual evapotranspiration and climatic water deficit has been explicitly included to account for the balance between fuel moisture and volume (e.g., refs. 50, 74, and 75). We used climatic water deficit here, but instead of actual evapotranspiration, we used temperature seasonality due to low correlation with other variables. Climatic water deficit is generally among the most important predictors of fire and forest structure (76), but temperature seasonality, or range, has also been a strong climatic driver of wildfire (77, 78). Although some ecoregion models performed worse than the statewide models, they were nevertheless more likely to predict increasing fire probability where there were larger areas of forests and other fire-prone vegetation, as expected.

Although maps of future wildfire conditions are highly desired for climate-resilient and ecologically sustainable management and resource allocation decisions, the model differences illustrated here highlight the notion that there is major uncertainty involved in predicting fire in the future, particularly for longer-term projections (58). Few FDM explicitly include vegetation-related variables to project future fire distributions, partly because future vegetation is difficult to predict. Not only will there be direct

influences of climate on plant species distributions (79), but future fire may also be reduced through current burning of vegetation (80); alternatively, certain plant species could increase fire activity if positive feedbacks are triggered with invasive species, which are primarily invasive annual grasses and forbs in California (81). Fire–climate–vegetation relationships will also likely be mediated, or disrupted, by human influences (28, 51, 59). The inability to seamlessly account for interactions and feedbacks among wildfires, climate, vegetation, and land use change, or interactions with other forest disturbances such as insect outbreaks, wind-throw, or drought-related mortality is a drawback to the statistical approach of FDM.

Our results suggest that developing FDMs with a geographical extent and scale that captures variation in fire regimes may be preferable to broader-scale models for making landscape-level decisions. Although smaller geographical extents limit the potential for transferring models onto different geographies, the advantage is that the models may better capture unique fire–environment relationships inherent to a specific region. These may also improve future forecasts restricted to those regions. There is great diversity in fire regimes worldwide, and there have been efforts to map them (82). Fire mapping at the scale of fire regimes is a result we would therefore expect to extend to any fire-prone region.

As Keeley and Syphard (58) said, “predicting future fire regimes is not rocket science; it is far more complicated than that.” Fire distribution models can be informative tools for delineating the parts of the landscape with the highest likelihood of burning and help establish priorities for management actions to preserve ecosystem function, biodiversity, and sustainable human communities. While there are a range of management approaches available, there has already been substantial research illustrating the potential benefits of different strategies in different locations. For example, in dry mixed-conifer forests, there are well-established cobenefits of strategic vegetation management and cultural burning practices that may not only reduce the potential for severe fire killing ecologically important older forests but may also reduce fire risk to communities in the vicinity (83). In coastal shrublands, where positive feedbacks between wildfire and invasive annual grasses have been widely documented, actions such as ignition prevention and invasive species management may best meet mutual objectives of protecting community safety while conserving biodiversity (4). Recent research shows that, despite the variety of factors that contribute to destructive wildfires, proximity to the WUI is by far the most important factor distinguishing fires that result in structure loss from those that do not (68). Therefore, land use planning to reduce human exposure to wildfire is another option with potential mutual benefits, not only in California but in fire-prone locations globally (15). Furthermore, regardless of geographic region, there is substantial evidence that homeowner mitigation actions can increase the likelihood that structures survive wildfires (84, 85). For fire management and policy decisions in an era of global change, the most important consideration for California and beyond is that one size does not fit all and that geography plays an important role in how and where fires will continue to burn.

Materials and Methods

Study Area and Ecoregions. The study area is the state of California (423,971 km²) which spans about 13 degrees of latitude and 4,000 m of elevation, including the lowest and highest points in the conterminous USA. Complex topography is primarily a result of recent tectonic activity. Both north-south and east-west trending mountain ranges ring the central valley, once a vast grassland and seasonal wetland, now almost entirely converted to agriculture (86). Annual precipitation ranges from >300 cm on the northwest coast to <5 cm in

the southern deserts, and the mountainous topography modifies precipitation patterns through orographic uplift and rain shadows (87). The Jepson Ecoregions (88) used in these analyses divide the state into major ecological regions sharing similar climate, topography, flora, and vegetation mosaics. Eighty percent of the state lies within the California Floristic Province—CFP (Northwestern, Cascade Range, Sierra Nevada, Great Valley, Central Western, and Southwestern ecoregions)—characterized by a Mediterranean-type climate (cool wet winters, warm dry summers) and exceptionally high plant diversity with 20% of all vascular plant species found in the United States, 37% of which are endemic (89, 90). Vegetation of the CFP spans chaparral (evergreen shrublands), coastal scrub, and oak woodlands and grasslands in the south and at lower elevations in valleys and foothills, to mixed evergreen, conifer, montane, and subalpine forests in the north and at higher elevations. The northeastern Modoc Plateau and East Sierra Nevada are part of the interior, cold-arid Great Basin Province, with dry forests, woodlands, and shrub-steppe vegetation. The southeastern Mojave and Sonoran Deserts are hot and arid, found in the Desert Province, and dominated by desert scrub vegetation, with some desert chaparral and dry woodland at higher elevations and near ecoregion boundaries (91). Most of the CFP is fire-prone due to moderate to high plant productivity combined with a lengthy dry season; consequently, many of the plants are adapted to the diverse fire regimes found there (92).

Response and Predictor Variables. We used fire perimeter data from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program [FRAP (93)]. These data provide the most comprehensive spatially explicit delineation of fire perimeters in the state, including most fires ≥ 10 acres (0.04 km²), although unburned islands within perimeters are typically not delineated (94). We selected perimeter data between 1981 and 2010 to match the temporal extent of baseline climate data used as predictors (see below). Previous fire distribution modeling approaches have used a variety of response variables, such as small or large fire occurrence, fire ignition location, fire frequency, or area burned. We focused here on occurrence of large fires, as this accounts for most fire activity without including fires that are so small that they delineate the location of ignitions, which have distinctly different spatial patterns than those of large fires or area burned (41, 50). We tested the sensitivity of our results to fire occurrence of two different sizes: ≥ 40 ha and ≥ 100 ha. After initially finding similarity in results, we continued using the dataset with fires ≥ 40 ha, as this size has been used to define "large fires" in previous studies (e.g., refs. 34, 60, and 78) and provided a larger sample size (3,902 vs. 2,787 fire perimeters).

To represent fire presence, we generated a random sample of points within fire perimeters. We determined the number of points per perimeter as the square root of the ratio between the area of a given fire and the smallest fire area [after (45)]. We also sampled fire absences by randomly distributing 14,220 points in unburned areas. We used these absences data in model validation (see below). Because we used Maxent models, we also sampled background data by randomly distributing 100,000 points throughout California.

We explored several predictor variables related to climate, terrain, and human infrastructure (*SI Appendix, Tables S3 and S4*). All predictor variables were cropped to the extent of California and resampled to 270 m resolution (*SI Appendix, Fig. S16*), which was the resolution of the climate data and the coarsest resolution of all the predictor variables. Our previous work suggests that 270 m is an appropriate scale for modeling climate-landscape phenomena in this region (95). For distance to all roads and principal roads, we calculated the nearest distance between roads and a cell of 270 m resolution. Distance to urban areas was derived from the land use data for 2010 sourced from the Integrated Climate and Land Use Scenarios (*SI Appendix, Table S3*). To do so, we selected those raster values related to low and high urban density (classes 13 and 14, respectively). Then we binarized land use data assuming 1 for those cells classified as low and high urban density (i.e., cell values of 13 and 14, respectively) and 0 for any other land use classes. ICLUS data were upscaled from 90 to 270 m by averaging the binarized values. We assumed as urban all those cells with $>0.50\%$ urban presences class; finally, we calculated the minimum distance of each cell to urban cells. Topographic heterogeneity was generated based on a 90-m digital elevation model by calculating the range in elevation of a focal cell and the three-cell radius around it. Finally, topographic heterogeneity was upscaled to 270 m resolution.

We performed a Pearson correlation analysis for all of California (*SI Appendix, Fig. S17*) and assumed highly correlated variables were those with $r > |0.7|$ (96).

Then, we calculated univariate Maxent models for the seven variables that showed high correlation (see details of Maxent model procedure below) and selected those that returned higher performance (*SI Appendix, Fig. S18*) for fire distribution modeling. We also performed a Pearson correlation analysis of the predictor variables for each ecoregion (*SI Appendix, Fig. S19*).

Fire Distribution Modeling. We constructed three types of FDM: (i) statewide FDM, (ii) statewide FDM with ecoregions, and (iii) ecoregion-specific FDM. The difference between (i) and (ii) is that the latter model used ecoregions as a categorical predictor variable in addition to the other environmental variables (*SI Appendix, Table S3*). We considered ecoregions as a categorical predictor variable to determine whether it would improve model performance over the statewide geographical extent without modeling individual ecoregions separately, which is what we did for (iii). We used Maxent (81) to construct FDMs for baseline climate conditions (1981 to 2010) and projected them to 2040 to 2069 and 2070 to 2099. Future conditions were defined by two global circulation models (GCMs) from the 5th Coupled Model Intercomparison Project, Centre National de Recherches Meteorologiques Coupled Global Climate Model, version 5 (CNRM-CM5) and Hadley Centre Global Environment Model version 2—Earth System model (HadGEM2-ES), and two representative concentration pathways (RCPs), RCP 4.5 and 8.5 (97) (*SI Appendix, Fig. S20*). We selected these GCMs because they are recommended for bracketing a wide range of climate conditions appropriate for California (98). They were downscaled to 270 m using the Basin Characterization Model (99).

Given that model hyperparameters could affect the degree of model complexity, performance, and geographical probability patterns (100, 101), we performed a sensitivity test to find the best hyperparameter combination for our datasets. For each model, we tested 189 hyperparameter combinations based on 21 regularization multiplier values ranging from 0.4 to 6 and nine combinations of features linear (L), quadratic (Q), hinge (H), product (P), and threshold (T) (i.e., LQH, LQP, LQT, QHP, QHT, HPT, LQHP, QHPT, and LQHPT). In addition, because two statewide models accounted for large presence-absence and background point datasets, we randomly sampled them to perform hyperparameter tuning (i.e., we used 7,110 presences, 7,110 absences, and 25,000 background points). After completing the hyperparameter tuning, new final models were run with entire datasets and the best hyperparameters.

Because we projected our model onto different time periods, we used spatially structured block-cross validation based on four partitions to evaluate model transferability more directly (102, 103). Given that the size of the blocks could affect how data are partitioned, we tested 70 different sizes between 25 and 135 km resolution. For each candidate size, we tested the spatial autocorrelation (measured by Moran's I), environmental similarity (based on Euclidean distance), and differences in the amount of data among partition groups (SD). The size that best fits the data was the one that equilibrated these three parameters [(104); *SI Appendix, Figs. S21 and S22*]. To be more rigorous with model validation, we fit models with presences and background points data for each partition but validated with presences and absences data. We used the AUC (Area Under the Curve), IMAE (Inverse Mean Absolute Error, calculated as 1-MAE) as threshold-independent performance metrics (105), and the TSS (True Skill Statistic), Sorensen, True Positive and True Negative Rate as threshold-dependent metrics (106) based on the threshold at which the sum of the sensitivity and specificity is the highest (107). We used complementary log-log probability for Maxent predictions (108).

In addition to reporting performance metrics, we also explored model performance in geographic space by mapping the difference between spatial predictions made by each FDM and the fire perimeters from 1981 to 2010 (fire probability = 1). Using this approach, high values correspond to areas where the FDM predicted high fire probability, but there was no fire during the study period, while low values indicate areas in which a fire occurred but were predicted to have low fire probability by the FDM. Values close to 0 indicate areas of agreement between the FDM and the fire perimeters (Fig. 1 G-I).

Calculating Variable Importance. To calculate variable importance for the FDM, we developed model predictions for each observation of the original occurrence and background data, representing the full model results. For each predictor variable, we permuted the values between observations, and a model prediction was made for each observation using the shuffled dataset for five permutations.

At each permutation, we computed a Pearson correlation between reference predictions and the predicted values from the shuffled data. The importance score is calculated as $1 - \text{correlation coefficient}$. The final variable importance score for each variable is expressed as a percentage of the sum of all mean scores. We used the R packages `biomod2`, `ecospat`, and `fitMaxnet` to calculate variable importance (109–111).

Exploring Fire Probability under Climate Change Scenarios. To summarize the predicted trends in fire probability under each climate change scenario and model-building procedure, we compared the fire probability-weighted area (km^2) across each ecoregion under each set of models and climate scenarios. This approach sums the continuous probability pixels within each ecoregion.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

- H. A. Kramer, M. H. Mockrin, P. M. Alexandre, V. C. Radeloff, High wildfire damage in interface communities in California. *Int. J. Wildland Fire* **28**, 641–650 (2019).
- S. Zabb-Parmley, Considering modern fire codes in replacing wood-shingle and wood-shake roofing. *APT Bull. J. Preserv. Technol.* **52**, 33–40 (2021).
- R. G. Fovell, A. Gallagher, An evaluation of surface wind and gust forecasts from the high-resolution rapid refresh model. *Weather Forecast* **37**, 1049–1068 (2022).
- J. E. Keeley, A. D. Syphard, Twenty-first century California, USA, wildfires: Fuel-dominated vs. wind-dominated fires. *Fire Ecol.* **15**, 1–15 (2019).
- H. Buechi, P. Weber, S. Heard, D. Cameron, A. J. Plantinga, Long-term trends in wildfire damages in California. *Int. J. Wildland Fire* **30**, 757–762 (2021).
- S. Hamideh, P. Sen, E. Fischer, Wildfire impacts on education and healthcare: Paradise, California, after the Camp Fire. *Nat. Hazards* **111**, 353–387 (2022).
- C. H. Guterman *et al.*, Vegetation type conversion in the US Southwest: Frontline observations and management responses. *Fire Ecol.* **18**, 1–16 (2022).
- A. D. Syphard, T. J. Brennan, H. Rustigian-Romsos, J. E. Keeley, Fire-driven vegetation type conversion in Southern California. *Ecol. Appl.* **32**, e2626 (2022).
- K. S. Hemes, C. A. Norlen, J. A. Wang, M. L. Goulden, C. B. Field, The magnitude and pace of photosynthetic recovery after wildfire in California ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2201954120 (2023).
- M. W. Jones *et al.*, Climate change increases the risk of wildfires. *ScienceBrief Rev.* **116**, 117 (2020).
- G. MacDonald *et al.*, Drivers of California's changing wildfires: A state-of-the-knowledge synthesis. *Int. J. Wildland Fire* **32**, 1039–1058 (2023).
- W. C. C. Greenberg, Relational Geographies of Urban Unsustainability: The 4 entanglement of California's Housing Crisis with WUI Growth and 5 Climate Chang. *Proc. Natl. Acad. Sci. U.S.A.*, in press.
- V. C. Radeloff *et al.*, Rapid growth of the US wildland-urban interface raises wildfire risk. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3314–3319 (2018).
- Agreement for Shared Stewardship of California's Forest and Rangelands. MOU between the State of California and the USDA Forest Service (2020). <https://www.gov.ca.gov/2020/08/13/california-u-s-forest-service-establish-shared-long-term-strategy-to-manage-forests-and-rangelands/>. Accessed 5 February 2024.
- M. A. Moritz *et al.*, Learning to coexist with wildfire. *Nature* **515**, 58–66 (2014).
- D. B. McWethy *et al.*, Landscape drivers of recent fire activity (2001–2017) in south-central Chile. *PLoS One* **13**, e0201195 (2018).
- S. L. Litteral, After the wildfires: PG&E, bankruptcy, and corporate sustainability. *Environ. Ecol. Pol'y* **43**, 119 (2020).
- W. J. Bond, B. van Wilgen, *Fire and Plants* (Chapman & Hall, 1996). Accessed 5 February 2024.
- A. D. Syphard, J. E. Keeley, Mapping fire regime ecoregions in California. *Int. J. Wildland Fire* **29**, 595–601 (2020).
- M. A. Moritz *et al.*, Climate change and disruptions to global fire activity. *Ecosphere* **3**, art49 (2012).
- J. G. Pausas, J. E. Keeley, A burning story: The role of fire in the history of life. *Bioscience* **59**, 593–601 (2009).
- J. E. D. Miller, H. D. Safford, Are plant community responses to wildfire contingent upon historical disturbance regimes? *Glob. Ecol. Biogeogr.* **29**, 1621–1633 (2020).
- J. E. Keeley, J. G. Pausas, P. W. Rundel, W. J. Bond, R. A. Bradstock, Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* **16**, 406–411 (2011).
- A. D. Miller, J. R. Thompson, A. J. Tepley, K. J. Anderson-Teixeira, Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. *Ecography* **42**, 55–66 (2019).
- T. J. H. Harrison Climate Change and California's Terrestrial Biodiversity. *Proc. Natl. Acad. Sci. U.S.A.*, in press.
- A. D. Syphard *et al.*, Human influence on California fire regimes. *Ecol. Appl.* **17**, 1388–402 (2007).
- J. W. van Wageningen, D. R. Cayan, Temporal and spatial distribution of lightning strikes in California in relation to large-scale weather patterns. *Fire Ecol.* **4**, 34–56 (2008).
- E. J. Fusco *et al.*, The human-grass-fire cycle: How people and invasives co-occur to drive fire regimes. *Front. Ecol. Environ.* **20**, 1–10 (2021).
- H. Safford, K. Van de Water, Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California (Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA 2014), p. 59.
- K. Anderson, *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources* (Univ. of California Press, 2005).
- S. L. Stephens, R. E. Martin, N. E. Clinton, Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. *For. Ecol. Manage.* **251**, 205–216 (2007).
- A. Klimaszewski-Patterson, P. J. Weisberg, S. A. Mensing, R. M. Scheller, Using paleolandscapes modeling to investigate the impact of Native American-set fires on pre-Columbian forests in the southern Sierra Nevada, California, USA. *Ann. Am. Assoc. Geogr.* **108**, 1635–1654 (2018).
- J. K. Shuman *et al.*, Reimagine fire science for the anthropocene. *PNAS Nexus* **1**, pga115 (2022).
- Conservation Biology Institute, "Modeling the Potential for Large High-Severity Fires in the Klamath Basin Region of California and Oregon and Their Potential Impacts on Marten and Fisher" (2019).
- A. L. Westerling, *Wildfire Simulations for California's Fourth Climate Change Assessment: Projecting Changes in Extreme Wildfire Events with a Warming Climate: A Report for California's Fourth Climate Change Assessment* (California Energy Commission Sacramento, CA, 2018), p. 57.
- J. Sathaye *et al.*, Estimating risk to California energy infrastructure from projected climate change (Publication CEC-500-2012-057, 2012), p. 60.
- M.-A. Parisien, D. A. Dawe, C. Miller, C. A. Stockdale, O. B. Armitage, Applications of simulation-based burn probability modelling: a review. *Int. J. Wildland Fire* **28**, 913–926 (2019).
- M. D. Flannigan, M. A. Krawchuk, W. J. de Groot, B. M. Wotton, L. M. Gouman, Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* **18**, 483–507 (2009).
- J. Franklin, *Mapping Species Distributions: Spatial Inference and Prediction* (Cambridge University Press).
- J. W. Williams, S. T. Jackson, Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**, 475–482 (2007).
- A. D. Syphard *et al.*, Predicting spatial patterns of fire on a southern California landscape. *Int. J. Wildland Fire* **17**, 602 (2008).
- M. A. Parisien, M. A. Moritz, Environmental controls on the distribution of wildfire at multiple spatial scales. *Ecol. Monogr.* **79**, 127–154 (2009).
- F. X. Catry, F. C. Rego, F. Bação, F. Moreira, Modeling and mapping wildfire ignition risk in Portugal. *Int. J. Wildland Fire* **18**, 921 (2009).
- M. Elia *et al.*, Estimating the probability of wildfire occurrence in Mediterranean landscapes using Artificial Neural Networks. *Environ. Impact Assess. Rev.* **85**, 106474 (2020).
- R. Davis, Z. Yang, A. Yost, C. Belongie, W. Cohen, The normal fire environment—Modeling environmental suitability for large forest wildfires using past, present, and future climate normals. *For. Ecol. Manage.* **390**, 173–186 (2017).
- J. L. Tracy *et al.*, Random subset feature selection for ecological niche models of wildfire activity in Western North America. *Ecol. Modell.* **383**, 52–68 (2018).
- M. L. Mann *et al.*, Incorporating anthropogenic influences into fire probability models: Effects of human activity and climate change on fire activity in California. *PLoS One* **11**, 1–21 (2016).
- N. Phelps, D. G. Woolford, Comparing calibrated statistical and machine learning methods for wildfire fire occurrence prediction: A case study of human-caused fires in La Caba Biche, Alberta, Canada. *Int. J. Wildland Fire* **30**, 850–870 (2021).
- J. E. Keeley, A. D. Syphard, Different historical fire-climate patterns in California. *Int. J. Wildland Fire* **26**, 253–268 (2017).
- A. D. Syphard *et al.*, The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes. *Global Environ. Change* **56**, 41–55 (2019).
- I. W. Park, M. L. Mann, L. E. Flint, A. L. Flint, M. Moritz, Relationships of climate, human activity, and fire history to spatiotemporal variation in annual fire probability across California. *PLoS One* **16**, e0254723 (2021).
- J. Harrison, S. Thorne, J. Safford, H. Hernandez, R. R. Franklin, Climate change and California's terrestrial biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 8672–8677.
- A. D. Syphard, J. E. Keeley, J. T. Abatzoglou, Trends and drivers of fire activity vary across California aridland ecosystems. *J. Arid. Environ.* **144**, 110–122 (2017).
- A. M. Lambert, C. M. D'Antonio, T. L. Dudley, Invasive species and fire in California ecosystems. *Fremontia* **38**, 29–36 (2010).
- Z. L. Steel, H. D. Safford, J. H. Viers, The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* **6**, 1–23 (2015).
- A. J. Das *et al.*, Empirically validated drought vulnerability mapping in the mixed conifer forests of the Sierra Nevada. *Ecol. Appl.* **32**, e2514 (2022).
- J. S. Littell, D. McKenzie, D. L. Peterson, A. L. Westerling, Climate and wildfire area burned in western U.S. ecoregions, 1916–2003. *Ecol. Appl.* **19**, 1003–1021 (2009).
- J. Keeley, A. Syphard, Climate change and future fire regimes: Examples from California. *Geosciences (Basel)* **6**, 37 (2016).
- A. D. Syphard, J. E. Keeley, A. H. Pfaff, K. Ferschweiler, Human presence diminishes the importance of climate in driving fire activity across the United States. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 13750–13755 (2017).
- J. G. Pausas, E. Ribeiro, The global fire-productivity relationship. *Global Ecol. Biogeogr.* **22**, 728–736 (2013).
- M. A. Krawchuk, M. A. Moritz, Constraints on global fire activity vary across a resource gradient. *Ecology* **92**, 121–132 (2011).
- J. G. Pausas, R. A. Bradstock, Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. *Global Ecol. Biogeogr.* **16**, 330–340 (2007).

ACKNOWLEDGMENTS. The University of California, Riverside, occupies the ancestral lands of the Cahuilla, Tongva, Luiseño, and Serrano peoples, and we are grateful for the opportunity to conduct this research on their homelands. We thank Alan and Lorrie Flint for providing the Basin Characterization Model hydroclimate data. This research was supported by NSF grant #1853697 and California Strategic Growth Council, Climate Change Research award #CCR30009.

Author affiliations: ^aConservation Biology Institute, Corvallis, OR 97333; ^bInstituto de Biología Subtropical, Consejo Nacional de Investigaciones Científicas y Técnicas - Universidad Nacional de Misiones, Puerto Iguazú, Misiones 3370, Argentina; ^cPrograma de Pós-Graduação em Biodiversidade Neotropical, Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, Paraná 85870-650, Brazil; ^dDepartment of Botany and Plant Sciences, University of California, Riverside, CA 92521; ^eDepartment of Geography, San Diego State University, San Diego, CA 92812; and ^fDepartment of Evolution, Ecology, and Organismal Biology, University of California, Riverside, CA 92521

63. J. E. Keeley *et al.*, Ignitions explain more than temperature or precipitation in driving Santa Ana wind fires. *Sci. Adv.* **7**, eabh2262 (2021).
64. M. A. Moritz, T. J. Moody, M. A. Krawchuk, M. Hughes, A. Hall, Spatial variation in extreme winds predicts large wildfire locations in chaparral ecosystems. *Geophys. Res. Lett.* **37**, 1–5 (2010).
65. J. H. Keeley, A. D. Syphard, Historical patterns of wildfire ignition sources in California ecosystems. *Int. J. Wildland Fire* **11**, 8779 (2018), 10.1071/WF18026.
66. S. Archibald, C. E. R. Lehmann, J. L. Gómez-dans, R. A. Bradstock, Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 6445–6447 (2013).
67. J. H. Scott, M. P. Thompson, J. W. Gilbertson-Day, Exploring how alternative mapping approaches influence firehazard assessment and human community exposure to wildfire. *GeoJournal* **82**, 201–215 (2017).
68. A. D. Syphard, J. E. Keeley, M. Gough, M. Lazarz, J. Rogan, What makes wildfires destructive in California? *Fire* **5**, 133 (2022).
69. H. D. Safford, A. K. Paulson, Z. L. Steel, D. J. N. Young, R. B. Wayman, The 2020 California fire season: A year like no other, a return to the past or a harbinger of the future? *Global Ecol. Biogeogr.* **31**, 2005–2025 (2022).
70. J. S. Littell, D. McKenzie, H. Y. Wan, S. A. Cushman, Climate change and future wildfire in the western United States: an ecological approach to nonstationarity. *Earths Future* **6**, 1097–1111 (2018).
71. A. L. Westerling *et al.*, Climate change and growth scenarios for California wildfire. *Clin. Change* **109**, 445–463 (2011).
72. M. Krawchuk, M. Moritz, "White Paper on Fire and climate change in California: Changes in the distribution and frequency of fire in climates of the future and recent past" (Publication 1911–2099, 2012); <https://escholarship.org/uc/item/5wd1797m>.
73. E. Batllori, M. A. Parisien, M. A. Krawchuk, M. A. Moritz, Climate change-induced shifts in fire for Mediterranean ecosystems. *Global Ecol. Biogeogr.* **22**, 1118–1129 (2013).
74. M. Mann *et al.*, Incorporating anthropogenic influences into fire probability models: Effects of human activity and climate change on fire activity in California. *PLoS One* **11**, e0153589 (2016).
75. A. D. Syphard, T. Sheehan, H. Rustigian-Romsos, K. Ferschweiler, Mapping future fire probability under climate change: Does vegetation matter? *PLoS One* **13**, e0201680 (2018).
76. V. R. Kane *et al.*, Water balance and topography predict fire and forest structure patterns. *For. Ecol. Manage* **338**, 1–13 (2015).
77. M. A. Krawchuk, M. A. Moritz, M.-A. Parisien, J. Van Dorn, K. Hayhoe, Global pyrogeography: The current and future distribution of wildfire. *PLoS One* **4**, e5102 (2009).
78. J. P. Argañaraz, G. Gavier Pizarro, M. Zak, L. M. Bellis, Fire regime, climate, and vegetation in the Sierras de Córdoba, Argentina. *Fire Ecol.* **11**, 55–73 (2015).
79. J. Franklin, J. M. Serra-Diaz, A. D. Syphard, H. M. Regan, Global change and terrestrial plant community dynamics. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 3725–3734 (2016).
80. M. D. Hurteau, S. Liang, A. L. R. Westerling, C. Wiedinmyer, Vegetation-fire feedback reduces projected area burned under climate change. *Sci. Rep.* **9**, 2838 (2019).
81. E. J. Fusco, J. T. Finn, J. K. Balch, R. C. Nagy, B. A. Bradley, Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 23594–23599 (2019).
82. S. Z. J. M. Pais, Global scale coupling of pyromes and fire regimes. *Commun. Earth Environ.* **4**, 267 (2023).
83. S. L. Stephens *et al.*, Fire and climate change: Conserving seasonally dry forests is still possible. *Front. Ecol. Environ.* **18**, 354–360 (2020).
84. A. D. Syphard, J. E. Keeley, Factors associated with structure loss in the 2013–2018 California wildfires. *Fire* **2**, 49 (2019).
85. M. A. Moritz *et al.*, Beyond a focus on fuel reduction in the WUI: The Need for regional wildfire mitigation to address multiple risks. *Front. Forests Global Change* **5**, 1–13 (2022).
86. A. T. Graham, R. C. O'Geen, "Geomorphology and soils" in *Ecosystems of California* (University of California Press, Oakland, CA, 2016), pp. 47–73.
87. M. Iacobelacobbis, S. F., Cayan, D. R., Abatzoglou, J. T. and Mooney, H., 2016, Climate, pp. 9–25 in Mooney, H., Zavaleta, E. Chapin, M. Iliis, S. F., Cayan, D. R., Abatzoglou, J. T. and Mooney, H., 2016, Climate, pp. 9–25 in Mooney, H., Zavaleta, E. Chapin, "Climate" in *Ecosystems of California*, M. Mooney, H., Zavaleta, E. Chapin, Ed. (Oakland, CA: University of California Press, 2016), pp. 9–25.
88. Jepson Flora Project, <https://ucjeps.berkeley.edu/efloral/>, Accessed 5 February 2024.
89. D. O. Burge *et al.*, Plant diversity and endemism in the California Floristic Province. *Madroño* **63**, 3–206 (2016).
90. J. Franklin, H. M. Regan, A. D. Syphard, A framework linking biogeography and species traits to plant species vulnerability under global change in Mediterranean-type ecosystems. *Front. Biogeogr.* **13**, e51254 (2021).
91. M. J. Barbour, J. Major, *Terrestrial Vegetation of California* (California Native Plant Society, 1990).
92. J. E. Keeley, H. D. Safford, *Fire As an Ecosystem Process: Chapter 3* (University of California Press, Oakland, CA, 2016).
93. California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP), <https://www.fire.ca.gov/Home/What-We-Do/Fire-Resource-Assessment-Program/GIS-Mapping-and-Data-Analytics>; fire perimeter data. Accessed 5 February 2024.
94. A. D. Syphard, J. E. Keeley, Historical reconstructions of California wildfires vary by data source. *Int. J. Wildland Fire* **25**, 1221–1227 (2016).
95. J. Franklin *et al.*, Modeling plant species distributions under future climates: How fine scale do climate projections need to be? *Glob. Chang. Biol.* **19**, 473–483 (2013).
96. C. F. Dormann *et al.*, Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46 (2013).
97. T. F. Stocker *et al.*, "Summary for Policymakers" in *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of IPCC Intergovernmental Panel on Climate Change*, C. B. Field *et al.*, Eds. (Cambridge University Press, Cambridge, UK; New York, NY, USA, 2012), pp. 1–19.
98. D. W. Pierce, D. R. Cayan, L. Dehann, "Creating climate projections to support the 4th California climate assessment" (University of California at San Diego, Scripps Institution of Oceanography: La Jolla, CA, USA, 2016), p. 20.
99. A. L. Flint, L. E. Flint, U.S.G.S., "Application of the basin characterization model to estimate in-place recharge and runoff potential in the Basin and Range carbonate-rock aquifer system, White Pine County, Nevada, and adjacent areas in Nevada and Utah" (U.S. Geological Survey Scientific Investigations Report 2007–509, 2007).
100. Y. Fourcade, Fine-tuning niche models matters in invasion ecology. A lesson from the land planarian *Obama nungara*. *Ecol. Modell* **457**, 109686 (2021).
101. N. S. Morales, I. C. Fernández, V. Baca-González, MaxEnt's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. *PeerJ* **5**, e3093 (2017).
102. D. R. Roberts *et al.*, Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**, 913–929 (2017).
103. L. Santini, A. Benítez-López, L. Maiorano, M. Čengić, M. A. J. Huijbregts, Assessing the reliability of species distribution projections in climate change research. *Divers. Distrib.* **27**, 1035–1050 (2021).
104. S. J. E. Velazco, F. Villalobos, F. Galvão, P. De Marco Júnior, A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. *Divers. Distrib.* **25**, 660–673 (2019).
105. K. Konwalik, A. Nosol, Evaluation metrics and validation of presence-only species distribution models based on distributional maps with varying coverage. *Sci. Rep.* **11**, 1–15 (2021).
106. S. J. E. Velazco, M. B. Rose, A. F. A. de Andrade, I. Minoli, J. Franklin, flexsdm: An R package for supporting a comprehensive and flexible species distribution modelling workflow. *Methods Ecol. Evol.* **13**, 1661–1669 (2022).
107. C. Liu, M. White, G. Newell, Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography* **34**, 232–243 (2011).
108. S. J. Phillips, R. P. Anderson, M. Dudík, R. E. Schapire, M. E. Blair, Opening the black box: An open-source release of Maxent. *Ecography* **40**, 887–893 (2017).
109. W. Thuiller *et al.*, Package 'biomod2': Species distribution modeling within an ensemble forecasting framework. *Ecography* **32**, 369–373 (2016).
110. V. Di Cola *et al.*, ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* **40**, 774–787 (2017).
111. Wilson, fitMaxnet: Fit MaxEnt Niche Models Using Maxnet (2023), <https://github.com/peterbat1/fit>. Accessed 5 February 2024.