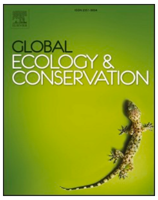
Global Ecology and Conservation 33 (2022) e01944

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Projecting the remaining habitat for the western spadefoot (*Spea hammondii*) in heavily urbanized southern California

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ARTICLE INFO

Keywords:
Integrated species distribution model
Point process model
Species status assessment
Amphibian conservation
Habitat fragmentation
Land cover change

ABSTRACT

Extensive urbanization in coastal southern California has reduced natural habitat in this biodiversity hotspot. To better conserve ecological communities, state and federal agencies, along with local jurisdictions and private stakeholders, developed regional conservation plans for southern California. Although many protected areas exist within this region, the patchwork nature of these protected areas might not provide good coverage for species that require multiple habitat components, such as amphibians with complex life histories. Because of declines in the past century, the status of the western spadefoot (*Spea hammondii*) in southern California is of concern to state and federal wildlife agencies. Species distribution models (SDMs) can aid in determining the conservation status of imperiled species by projecting where suitable habitat remains and how much is protected from further development. We built SDMs that integrated site-occupancy data from systematic pitfall trapping surveys and presence-only data from biodiversity databases and citizen science platforms to project the current distribution of western spadefoots in southern California. Western spadefoot occurrence was positively related to the cover of grassland or shrub/scrub and the % sand in the soil within a 1000 m buffer, and was negatively related to slope, elevation, and distance to ephemeral streams or vernal pools. Most of the remaining unprotected habitat for western spadefoots is in the southern half of its historical range in western San Diego and Riverside counties. A few large tracts of spadefoot habitat exist on U.S. Department of Defense lands and smaller tracts remain on ecological reserves owned by state and local government agencies. Only small patches of habitat remain in the northern half of this clade's historical range in Ventura, Orange, Los Angeles, and San Bernardino counties. Existing regional conservation plans provide ostensible spatial coverage of the majority of extant habitat for western spadefoots in southern California, but most of the habitat within the jurisdiction of these plans lacks formal protection, exposing this species to further declines as urbanization continues in the 21st century.

Abbreviations: PPM, Point process model; SSA, Species status assessment; SDM, Species Distribution Model; LCC, Land cover change.

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https://doi.org/10.1016/j.gecco.2021.e01944
Received 24 July 2020; Received in revised form 3 November 2021; Accepted 27 November 2021
Available online 29 November 2021
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1. Introduction

Anthropogenic land cover change and habitat fragmentation has left many species to persist in small protected areas or remaining patches of undeveloped open space. For species in fragmented habitats, the landscape context surrounding historically occupied sites can be a primary determinant of where populations persist (Fischer and Lindenmayer, 2007), and regional conservation plans might be needed to ensure a network of ecologically connected protected areas provide sufficient habitat. Coastal southern California presents a challenge for conservation planning because high native biodiversity coincides with the second-most populated metropolitan region of the United States of America (Hunter et al., 2003; Tracey et al., 2018b; Census Bureau,). Rapid urbanization and sprawl in the last century has caused many species to be threatened with extinction within this part of the California Floristic Province biodiversity hotspot (Myers et al., 2000). In response, the state of California initiated the Natural Communities Conservation Planning (NCCP) program in the early 1990s to conserve California's ecological communities. The NCCP program, along with Habitat Conservation Plans (HCPs) under the federal Endangered Species Act, have led to the creation of many protected areas in coastal southern California within and surrounding developed areas of high human population density (Franklin et al., 2011; Pollak, 2001). Similar to the rest of the United States (UNEP-WCMC and IUCN 2018), many of the protected areas in southern California are small (< 1 km^2, Mitrovich et al., 2018, Tracey et al., 2018b). The reserve system in southern California was driven by the conservation of a few umbrella species (Franklin et al., 2011; Pollak, 2001) and therefore might not support viable populations for some non-target species with different habitat needs (Brashares et al., 2001; Fisher et al., 2002; Mitrovich et al., 2018; Ordeñana et al., 2010).

In urbanized and fragmented landscapes, species with complex life histories, including many amphibians, can be especially susceptible to loss of genetic diversity, declines, and extirpation (Noël et al., 2007; Rubbo and Kiesecker, 2005; Semlitsch, 2000). The susceptibility of amphibians to fragmentation is often tied to the disconnect between the different habitats required for each life stage (Becker et al., 2007). Dependence on multiple habitats has made amphibians more susceptible to land cover change than larger megafauna which would be predicted to be impacted more heavily (Burdett et al., 2010; Tracey et al., 2018a). Therefore, there is a need to evaluate how well regional conservation plans designed for other taxa are protecting habitat for native amphibians. Western spadefoots (*Spea hammondii*), which breed in coastal southern California's ephemeral aquatic habitats (Baumberger et al., 2020), are a species of conservation concern for which the utility of multi-species conservation plans is unknown. Although western spadefoots spend the majority of their adult life in terrestrial habitats, they must return to vernal pools to breed during the rainy season (Baumberger et al., 2019; Stebbins, 2003) and they may be particularly susceptible to habitat fragmentation and conservation design that severs the connectivity between adult and breeding habitat (Brehme et al., 2018). Because of declines in the Central Valley (Fisher and Shaffer, 1996) and southern California, western spadefoots are a species of special concern in California (Jennings and Hayes, 1994; Thomson et al., 2016) and are currently undergoing a status review by the U.S. Fish and Wildlife Service, 2015. The status of this species in southern California is of particular interest because a recent study concluded that western spadefoots in this region represent a genetically and ecologically distinct clade from the more widely distributed northern clade (Neal et al., 2018). Population viability analysis has been used to evaluate whether species necessitate protection under the U.S. Endangered Species Act (McGowan et al., 2017). Demographic and abundance data are not available for western spadefoots, however. When population-level data are lacking, modeling the distribution of suitable habitat can provide an indicator of species status (Cuevas-Yáñez et al., 2015; Syfert et al., 2014). Assessing where contiguous tracts of habitat remain for declining species in heavily urbanized landscapes requires modeling habitat suitability at a broad scale while accounting for the landscape context around habitat patches (Mitrovich et al., 2018; Neal et al., 2020; Rose et al., 2020; Tracey et al., 2018a).

Species Distribution Models (SDMs) are commonly used for conservation decisions (Guisan et al., 2013), but like any empirical modeling effort, SDMs are only as good as the data used to fit them. Abundant "presence-only" data on species occurrence available from online databases are unable to provide estimates of species occurrence probabilities (Hastie and Fithian, 2013), and are often spatially-biased (Dickinson et al., 2010), leading to improper inferences about species-environment relationships (Fithian et al., 2015). Recent developments enable researchers to integrate abundant presence-only data with more limited, but higher quality data from systematic detection/non-detection surveys (Fletcher et al., 2019). Integrating multiple data sources enables fitting models that reduce the effects of spatial sampling bias in presence-only data, estimate ecologically relevant parameters such as the probability of occurrence or expected count of individuals of the focal species, and produce better predictions than models fit to single data sources (Fithian et al., 2015; Koshkina et al., 2017). Because decisions about future survey efforts, listing status, and identification of critical habitat can be made based in part on the projections from SDMs, it is vital that models integrate all available data and produce unbiased estimates of a species' distribution. SDMs previously developed for western spadefoots in southern California focused on climatic determinants of the species' range (Neal et al., 2018) or were fit using a single data source (Franklin et al., 2009). A recent study on the northern clade of the western spadefoot demonstrated how integrating multiple data sources could lead to improved projections of remaining habitat (Rose et al., 2020). A SDM that integrates multiple data sources and includes landscape covariates on occurrence has crucial implications for assessing the status of the genetically distinct western spadefoot clade in southern California.

In this study, we created a SDM for the western spadefoot in southern California. We integrated systematic site-occupancy survey data with presence-only data to quantify the relationships between landscape-level covariates and spadefoot occurrence while accounting for spatial sampling bias in the input data. Our goals were to: 1) project where habitat remains for western spadefoots in this fragmented landscape, 2) quantify how much of this species' habitat is currently in protected areas, 3) identify unprotected tracts of habitat that could lower the risk of extirpation if conserved, and 4) identify areas without recent observations that could be targeted for future surveys to document western spadefoot occurrence. Our results provide valuable information about the current distribution of western spadefoots in southern California and highlight both the value and current limitations of regional conservation plans for protecting this declining species.

2. Methods

2.1. Study region and species

The southern clade of the western spadefoot is found in coastal southern California, south of the Transverse ranges in Ventura, Los Angeles, Orange, Riverside, San Bernardino, and San Diego counties (Fig. 1). Vernal pools and associated open habitats historically occupied by western spadefoots have been heavily affected by urbanization (Mattoni and Longcore, 1997; U.S. Fish and Wildlife Service, 2005; Bauder et al., 1998) Development in coastal southern California has converted much of the low elevation coastal and inland valley habitats to urban and suburban environments (e.g., Hunter et al., 2003, Bagan and Yamagata, 2014), resulting in the extirpation of western spadefoots from large parts of their historic range, such as the Los Angeles Basin (Jennings and Hayes, 1994; Mattoni and Longcore, 1997; Morey, 2005; Neal et al., 2020). Open habitats preferred by western spadefoots including grassland, coastal scrub, chaparral, and oak woodland (Morey, 2005) still exist at mid-elevation outside of major urban areas (Xian et al., 2009). Western spadefoots primarily breed in vernal pools, pools associated with ephemeral streams, and other seasonally-filled bodies of water and larval development can take from 4 to 11 weeks (Morey, 1998). Non-native predators such as the American bullfrog (*Lithobates catesbeianus*) pose a potential threat to western spadefoots, but the ephemeral nature of pools used by western spadefoots for breeding can provide a refuge from larger predators (Morey, 2005). Western spadefoots spend the majority of the year aestivating underground in burrows that they dig with the eponymous spades on their hind feet. Radio-tracking of western spadefoots in two sites in southern California showed that individuals prefer to burrow in soils with higher sand and silt content and avoid sites with high clay content (Baumberger et al., 2019). The life-history of western spadefoots necessitates both suitable breeding pools and adjacent upland habitat for aestivation during the long, hot dry season.

2.2. Data collection

As part of a larger study of the response of small vertebrates to habitat fragmentation in southern California, pitfall traps were placed along gradients of rainfall, elevation, and human disturbance (Amburgey et al., 2021; Case and Fisher, 2001; Franklin et al.,

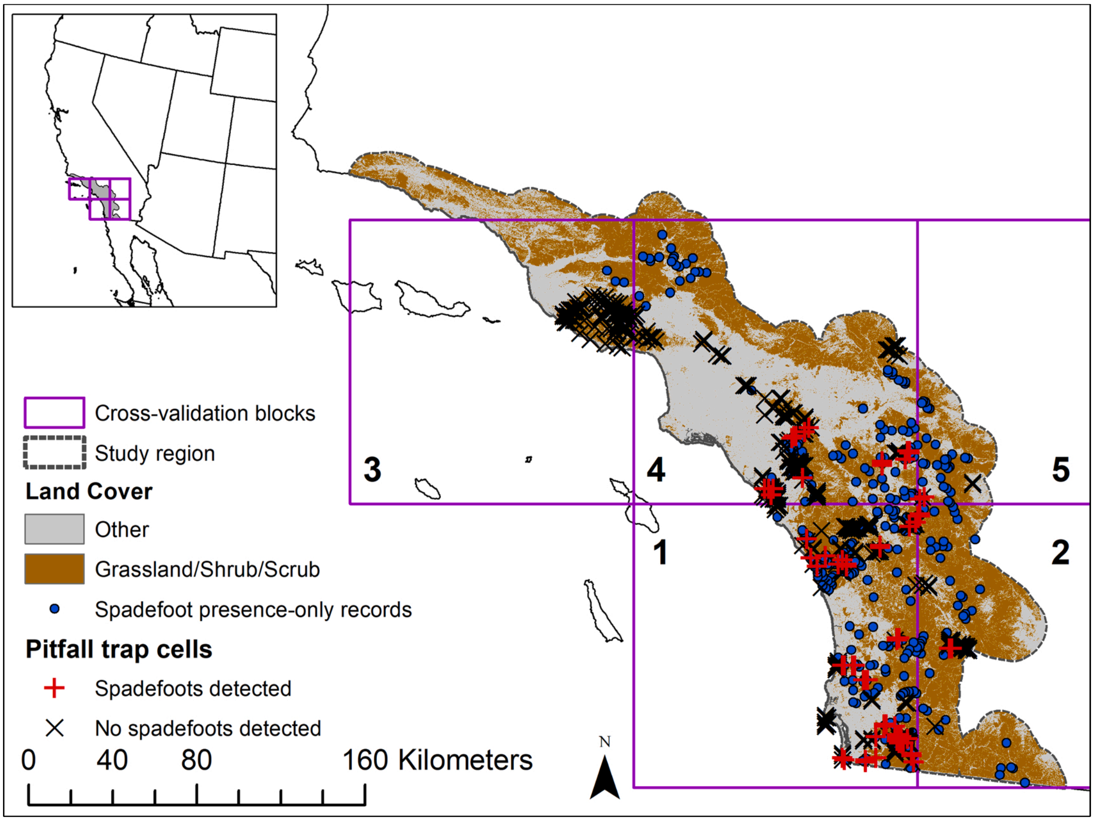

Fig. 1. Map of pitfall trap locations and presence-only records for western spadefoots (*Spea hammondii*) in coastal southern California. Black Xs indicate 1 km^2 cells with pitfall trap arrays with no western spadefoot detections, red + symbols indicate 1 km^2 cells with pitfall trap arrays where western spadefoots were detected. Square purple blocks are the spatial blocks used for model cross-validation, each with its own identifying number. Grassland and shrub/scrub land cover data are from the 2016 National Land Cover Dataset (Yang et al., 2018). The study region is the historical range of western spadefoots buffered by 10 km.

2009; Fisher et al., 2008). We deployed pitfall traps in 804 drift-fence arrays distributed throughout the range of the western spadefoot in southern California from 1995 to 2016. Because pitfall trap arrays were often spatially clustered, we compiled the detection/non-detection data for all pitfall trap arrays within a grid of 1 km x 1 km cells, resulting in 376 sampled cells. The number of trap arrays per cell ranged from 1 to 13 (mean = 2.1 arrays per cell, SD = 1.7 arrays), and cells were trapped from 2 to 18 years (mean = 5.7 years, SD = 3.1 years). These pitfall trapping data can be analyzed in an occupancy framework because sites were trapped for several years and the detection history (1 if spadefoots were detected, 0 if not) was recorded for each array on each sampling occasion.

We compiled western spadefoot occurrence records from vernal pool surveys conducted by the Western Riverside County Regional Conservation Authority from 2008 to 2016 in western Riverside County, California; field survey data from Marine Corps Base Camp Pendleton, San Diego; and U.S. Geological Survey (USGS) stream surveys for amphibians in Ventura, Los Angeles, San Diego, Riverside, San Bernardino, and Orange counties from 2000 to 2016. We also compiled presence-only records of western spadefoots in the southern range from the California Department of Fish and Wildlife's (CDFW) California Natural Diversity Database (CNDDB; California Department of Fish and Wildlife, 2020a), data developed for the California Amphibian and Reptile Species of Special Concern analysis (Thomson et al., 2016), the citizen science platforms NAHerp (www.naherp.com) and HerpMapper (www.herpmapper.org), and published literature (Neal et al., 2018) collected from 1995 to 2016, to match the time period of pitfall trapping. We classify all of these data as presence-only because they lack sufficient information to characterize spatial survey effort and non-detection of western spadefoots. When duplicate records (identical spatial coordinates) existed in the presence-only data, we retained only the most recent western spadefoot occurrence from that location. We spatially thinned presence-only records using the "spThin" R package such that no two records were < 1 km apart to prevent overfitting of the model to locations with more reports of western spadefoots (Aiello-Lammens et al., 2015). This thinning resulted in a final dataset of 324 presence-only records reported from 1995 to 2016 from seven sources (Table A1). Finally, we constructed a 1 km x 1 km grid of background points (quadrature points) throughout the study area for use as a comparison to the presence-only data in the integrated Presence-Background Site-Occupancy (PB-SO) model (see *Integrated species distribution models* below). We also compiled 85 presence-only records collected from 2017 to 2020 as an independent dataset for testing model predictions (Table A2).

2.3. *Environmental predictors*

Western spadefoots breed in seasonal and ephemeral bodies of water, including streams, vernal pools, and small ponds (Stebbins, 2003), and capturing the distribution of these breeding habitats could lead to better SDMs. We extracted GIS data on ephemeral streams in the National Hydrography Dataset (U.S. Geological Survey 2019). We compiled GIS data on the distribution of vernal pools in the study region from federal (Marine Corps Base and Marine Corps Air Station Camp Pendleton, 2018; U.S. Fish and Wildlife Service, 2005; Marine Corps Air Station Miramar, 2018), state (California Department of Fish and Wildlife, 2020b), and local resource management agencies (City of San Diego Planning Department, 2019; County of Riverside Transportation and Land Management Agency, 2003), and supplemented vernal pool data with the distribution of seasonal and temporary palustrine wetlands from the National Wetlands Inventory (U.S. Fish and Wildlife Service, 2019) and playas and intermittent ponds from the National Hydrography Dataset (U.S. Geological Survey, 2019a). We calculated the distance to the nearest ephemeral stream and vernal pool or pond for each pitfall trapping site, presence-only record, and background point using the "rgeos" package (Bivand and Rundel, 2019) in R version 3.6.3 (R Core Team, 2020). We then used the compiled vector datasets on the distribution of suitable aquatic breeding habitats described above to create two rasters representing 1) the distance to the nearest ephemeral stream and 2) distance to the nearest vernal pool, ephemeral pond, or seasonal pond using the Euclidean Distance tool in ArcMap version 10.7.1 (Environmental Systems Research Institute, 2019b).

We compiled land cover data for the study region from the 2016 National Land Cover Dataset (NLCD) from the Multi-Resolution Land Characteristics Consortium (Yang et al., 2018). We created binary rasters of the distribution of grassland and shrub/scrub land cover: each 30 m x 30 m cell was given a value of 1 if it was classified as grassland/herbaceous or shrub/scrub, or a value of 0 if it was any other land cover. We repeated this for each year with NLCD data available: 2001, 2004, 2006, 2008, 2011, 2013, and 2016. We grouped grassland and shrub/scrub because western spadefoots prefer these open habitats (Stebbins, 2003) and although the area of southern California classified as grassland or shrub/scrub in the NLCD changed between years, the area classified as either grassland or shrub/scrub was highly consistent from 2001 to 2016. Comparing NLCD data from 2016 to 2001, $> 96\%$ of 30 m cells in our study area classified as grassland or shrub/scrub in 2001 were also classified as grassland or shrub/scrub in 2016. For each spadefoot presence-only record, pitfall trapping site, and background point, we calculated the proportion of the surrounding landscape that was classified as grassland or shrub/scrub within six concentric buffers of increasing size (100 m, 200 m, 500 m, 1000 m, 2000 m, and 5000 m). For presence-only records, we assigned to that site the proportion of grassland or shrub/scrub land cover from the classification nearest to the year in which the spadefoot presence was recorded. For pitfall trapping sites, we used land cover data from the median year of sampling for model fitting. For background points, we used the mean of the grassland or shrub/scrub cover over the study period from 2001 to 2016. We did not use any other land cover covariates, such as the proportion of developed land near a site, because they were highly correlated to the grassland and shrub/scrub land cover, and preliminary modeling showed that including additional land cover covariates led to worse predictive ability.

Western spadefoots prefer to burrow in sandy, friable soils and most western spadefoot burrows are in the upper 50 cm of soil (Baumberger et al., 2019). We calculated the % sand in the upper 50 cm of the soil for the study region from the gridded soil survey geographic database (gSSURGO; Soil Survey Staff, USDA 2019), producing a raster with 30 m x 30 m cells. For each pitfall trap sampling site, presence-only occurrence, and background point, we then calculated the % of sand in the upper 50 cm of the soil within the six buffers described above, by calculating the mean of the % sand in each 30 m raster cell. Finally, we calculated the elevation and slope at each pitfall trap site, presence-only occurrence, and background point from the U.S. Geological Survey's National Elevation Dataset (U.S. Geological Survey, 2019b). We calculated slope from a 1/3″ digital elevation model, and then aggregated the slope and elevation rasters to 1000 m resolution using the "raster" function from the raster R package (Hijmans, 2019) and calculating the mean of the 1000 m cells, to match the other predictor rasters. We included elevation as a predictor in the integrated SDM because most development in southern California has taken place at low elevations and open habitats favored by western spadefoots still exist at mid-elevations (Xian et al., 2009). Likewise, we included slope as a covariate because the temporary pools used by western spadefoots for breeding are unlikely to be found in areas with a higher degree of slope, and a previous model of the northern distribution of this species found that occurrence was most likely at areas of intermediate slope (Rose et al., 2020).

Environmental variables could influence detection of western spadefoots as well as occurrence. Pitfall traps capture adult western spadefoots, which are more likely to be active and moving on the surface during or after recent rainfall (Baumberger et al., 2019). In a drought year, adults might spend little time active on the surface and therefore be unavailable for detection during surveys. We downloaded monthly precipitation data from 1994 to 2016 from the PRISM dataset (PRISM Climate Group, 2016) and summed the monthly precipitation for each water year, from October through September. Because occurrence records are often biased towards accessible areas with high human population density, we included the distance to major roads and the distance to urbanized areas as covariates of observation for presence-only data. We compiled data on primary and secondary highways from the TIGER/LINE shapefiles produced by the U.S. Census Bureau (https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html). We used vector data on the location of urbanized areas (minimum population of 2500) from the U.S. National Atlas, compiled by ESRI (Environmental Systems Research Institute, 2019a), to calculate the distance presence-only records are from human population centers. We created distance to road and distance to urbanized area rasters using the Euclidean distance tool in ArcGIS version 10.7.1 (Environmental Systems Research Institute, 2019b).

For each 1 km^2 grid cell within which pitfall trapping data were compiled, we extracted environmental covariates for each individual pitfall trap array based on its coordinates, and then calculated the mean value of each covariate for all pitfall trap arrays within the same 1 km^2 cell. All environmental covariates used to fit integrated SDMs were standardized to have a mean of zero and a standard deviation of one to improve model convergence.

2.4. *Integrated species distribution models*

We fit species distribution models that integrated the results of systematic pitfall trapping surveys with presence-only records of western spadefoots in the study region. Using the methods of Koshkina et al. (2017), we fit models that enable disentangling the observation process (detection and reporting) from the ecological process determining where western spadefoots occur. We compiled all trapping data within each 1 km x 1 km grid cell within a year to create a binary detected (1) or not (0) response for each year of trapping. We then modeled the probability of spadefoot occurrence within each 1 km^2 cell at some point during the period in which it was trapped using a site-occupancy (SO) model that accounts for the imperfect detection of individual surveys (Appendix A1). Although this differs from the traditional use of single-season occupancy models, the seasonal and annual variation in spadefoot activity and reproductive effort means that individuals can easily go undetected at a site in a given year. Effectively, our model treats occupancy as the probability a cell was occupied by western spadefoots at some point during the survey period, following the broader definition of Latif et al. (2016). We inspected the detection history of pitfall trapping for each cell and counted how many cells had western spadefoot detections separated by one or more years of non-detection (i.e., a 1,0,…,1 pattern of detection) to assess if non-detection in some years was common at occupied sites.

We included the trapping effort each year (number of trap-nights per array) and the total amount of precipitation that fell during the corresponding water year as covariates on detection probability at site i (where site i is a 1 km^2 cell) in year t ($p_{i,t}$) in the SO model (Eq. 1), where γ_0 is the intercept, γ_{eff} is the effect of trapping effort at site i in year t ($\text{t.eff}_{i,t}$) on $p_{i,t}$, and γ_{ppt} is the effect of total annual precipitation at site i in year t ($\text{ann.ppt}_{i,t}$) on $p_{i,t}$.

$$logit(p_{i,t}) = \gamma_0 + \gamma_{eff} * t.eff_{i,t} + \gamma_{ppt} * ann.ppt_{i,t} \tag{1}$$

The observation process in the presence-background (PB) model for presence-only data is different from the detection process in the SO model: observation of presence-only records is a function of where people are most likely to survey for and report observations of western spadefoots (Fithian et al., 2015). Instead of non-detection data, the PB model requires background points covering the entire study region to act as quadrature points in an inhomogeneous Poisson Point Process model (Renner et al., 2015). These background points are contrasted with presence-only records to quantify how the environmental predictors influence spadefoot occurrence and how spatial sampling bias parameters influence presence-only reporting. We defined background points on a 1 km x 1 km grid throughout the study area, because this spatial resolution has been found to be sufficient to stabilize model performance in other studies (Renner et al., 2015; Warton and Shepherd, 2010) and produced good predictions in a study of western spadefoot distribution in northern California (Rose et al., 2020). Detection in the PB model incorporates distance to major roads and urbanized areas as two potential correlates of sampling bias (Eq. 2), where $b(s)$ is the probability of a spadefoot presence being detected (reported), α_0 is the intercept, α_{rd} is the effect of distance to road (rd.dist) on detection, and α_{urb} is the effect of distance to urbanized area (urb.dist) on detection.

$$log(b(s)) = \alpha_0 + \alpha_{rd} * rd.dist + \alpha_{urb} * urb.dist \tag{2}$$

Although the SO and PB models have different detection/observation process models, both inform the ecological process model of species occurrence in the integrated SDM, because the likelihoods for both models include the intensity, $\lambda(s)$, the ecological response variable in the integrated SDM (Eq. 3; Appendix A1). The intensity, $\lambda(s)$, is the expected number of individuals observed per unit area near location s, where s is a point location within the study area. In other words, $\lambda(s)$ is analogous to a density, the expected count of individuals within a defined area. The intensity for western spadefoots is a function of slope, elevation (elev), % sand (sand), grassland or shrub/scrub cover (gs), distance to ephemeral stream (eph.dist), and distance to vernal pool or temporary pond (vp.dist) (Eq. 3). Because the same environmental predictors of intensity are used for both the PB and SO data, both data sources inform the model's estimates of the β parameters and therefore the expected distribution of western spadefoots on the landscape.

$$\begin{aligned} log(\lambda(s)) = & \beta_0 + \beta_{sl} * slope + \beta_{sl2} * slope^2 + \beta_{el} * elev + \beta_{el2} * elev^2 + \beta_{sn} * sand + \beta_{sn2} * sand^2 + \beta_{gs} * gs + \beta_{gs2} * gs^2 + \beta_{eph} * eph.dist \\ & + \beta_{vp} * vp.dist \end{aligned} \tag{3}$$

The detection process model for the SO data (Eq. 1) and the log-linear model of species intensity (Eq. 3) are both components of the likelihood for the SO model (see Appendix A1). For the PB data, the observation process model (Eq. 2) and species intensity model (Eq. 3) are multiplied to obtain the expected number of detected presences at location s (Eq. 4). Eq. (4) represents a thinned Poisson process that accounts for the fact that only a fraction of all individuals are observed in the presence-only data, and the observation process (Eq. 2) results in a smaller number of individuals being observed near location s, $v(s)$ than would be expected based the intensity, $\lambda(s)$ alone (Fithian et al., 2015). In other words, $v(s)$ is the combined ecological and observation process that produces the presence-only data, and with the PB model we attempt to estimate the response variable of interest, $\lambda(s)$, by modeling the sampling bias in the observation process with $b(s)$.

$$v(s) = \lambda(s)b(s) \tag{4}$$

Our ability to estimate $\lambda(s)$ separately from the detection/observation processes is further enhanced by the fact that $\lambda(s)$ is part of the likelihoods for the PB and SO models (Appendix A1). To fit the integrated SDM, we modified the likelihood functions for the PB and SO models published by Koshkina et al. (2017) and estimated parameters by maximum likelihood (see Appendix A1 for the likelihood functions) using the "optim" function in R version 3.6.3 (R Core Team, 2020).

To translate the intensity, $\lambda(s)$ into occupancy probability for each 1 km^2 cell in our study area (ψ_i), we used the following equation (Eq. 5) from Koshkina et al. (2017) which integrates intensity over the area of site i (e.g., a 1 km^2 cell) to calculate the occupancy probability (ψ_i) at that site.

$$\psi_i = 1 - exp\left(- \int_i \lambda(s) ds \right) \tag{5}$$

Given our study's goals, we sought to create models with simple parametric relationships to avoid overfitting, which can lead to poor model predictions (Merow et al., 2014), such as unsampled habitat incorrectly being predicted to be unsuitable (Kramer-Schadt et al., 2013). Because we were concerned about overfitting the model to input data and thus producing poor estimates of spadefoot occurrence in unsampled areas, we used only linear and quadratic effects of environmental predictor variables following Rose et al. (2020). We did not include quadratic effects of the distance to vernal pools and distance to ephemeral streams in our models because preliminary model fitting produced unrealistic quadratic relationships for these predictors, with rapidly increasing probability of spadefoot occurrence at very large distances from these aquatic features. We evaluated the importance of environmental covariates on occupancy and detection by using the mean parameter estimate and standard error (SE) to calculate 95% confidence intervals ($\bar{x} \pm 1.96$ *SE) and how much those confidence intervals overlapped zero.

There is much uncertainty in the input data and predictions from SDMs, and some authors have argued that studies should provide an estimate of the spatial distribution of uncertainty to aid in interpretation of predicted species distributions (Rocchini et al., 2011). To visualize uncertainty in predicted probability of western spadefoot occupancy from the integrated SDM, we produced a map of the width of the 95% confidence interval (CI) of the predicted value of ψ. We took 1000 bootstrapped samples of model coefficients based on the mean parameter estimates and the variance-covariance matrix from the integrated SDM. We then calculated 1000 predictions of ψ for the study area and took the 2.5th and 97.5th percentile estimates of ψ for each cell to calculate the 95% CI for predicted occupancy probability.

2.5. Model projection and evaluation

To project the predictions of western spadefoot occupancy from the integrated SDM, we used the "predict.pbso" function from Koshkina et al. (2017) to calculate ψ using the coefficients from the best model (as defined below) and rasters containing the environmental covariate for the study region. We used the distance to aquatic feature rasters for projecting the distribution of spadefoot occupancy. Distance to urbanized areas and major roads were not included in model projections because these were covariates of the reporting of presence-only records. To prevent overfitting to training data and evaluate the integrated SDM's ability to project into novel environments, we used blocked cross-validation to choose the best performing model (Roberts et al., 2017). We divided the study area into five square blocks each measuring 135 km x 135 km. Then we performed a five-fold cross-validation in which all data sources (detection/non-detection, presence-only records, and background points) from four blocks were used to fit the model, and all data sources from the fifth block were withheld from training. The detection/non-detection data from the withheld block was then used for testing model predictions. This process was repeated with each block withheld in turn, and the predictive performance averaged over the five testing blocks. For comparison, we also evaluated predictions on training detection/non-detection data used to fit the model (i.e., the detection/non-detection data from four blocks) and five-fold random cross-validation. We evaluated model predictions and chose optimal buffer distances and weighting of data sources using the predictive log-likelihood. The predictive log-likelihood is a measure of model calibration, or the relationship between model predictions (continuous probability of occurrence, between 0 and 1) and observed data (binary detected or not, 1 or 0) (Fithian et al., 2015; Lawson et al., 2014). To evaluate model discrimination, the ability of the model to distinguish presences from absences, and to provide an alternative metric for comparison to the predictive log-likelihood we also calculated the area under the receiver operating characteristic curve (AUC). We compared integrated SDMs that varied in two parameters: 1) the buffer distance for landscape-level covariates (% sand and grassland/shrub land cover), and 2) the relative weighting of PB vs. SO data in the joint likelihood. We first fit models using different buffer distances for landscape-level

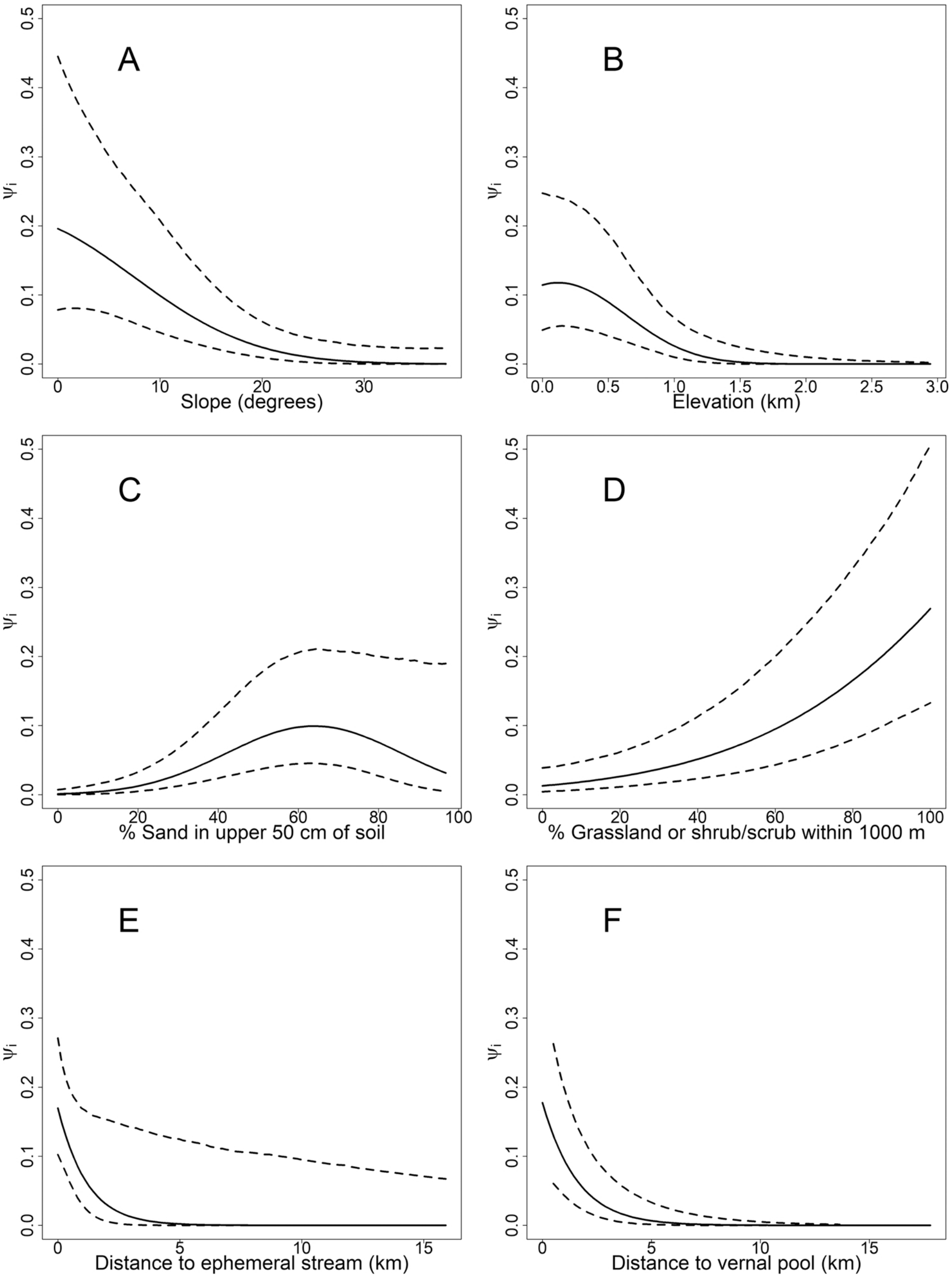

Fig. 2. Marginal response curves displaying the probability of western spadefoot (*Spea hammondii*) occurrence, ψ_i, vs. varying levels of environmental predictors. For each plot, the value of the predictor is varied on the x-axis, and all other predictors are held constant at their average value. Solid lines are predicted mean relationships, dashed lines are 95% bootstrapped confidence intervals. Predictions are presented ranging from the minimum to maximum observed value in the study area.

covariates (land cover and % sand in the upper 50 cm of soil), and selected the best model based on its ability to predict withheld SO data in the blocked cross-validation, giving equal weight to each data type. Because presence-only data and systematic SO data might differ in their quality (e.g., precision of location, certainty of identification), we then used the optimal buffer distance and tested how preferentially weighting these two data sources in the integrated SDM affected the quality of predictions, following Fletcher et al. (2019). The weight given to SO data in the joint likelihood was varied from 0.05 to 0.95 in increments of 0.05 and the predictive ability of the SDM in blocked cross-validation was evaluated for each weighting. We chose the best model based on the buffer distance and data weighting that produced the highest predictive log-likelihood, and used the best model to project the predicted probability of occurrence (ψ, ranging from 0 to 1) of western spadefoots in southern California. Finally, we evaluated the ability of the best model to predict presence-only records reported from 2017 to 2020 (that were not used to fit the model) using presence-background AUC, because no non-detection data was available to calculate log-likelihood, a prevalence-dependent metric (Lawson et al., 2014). All SDMs were fit in R version 3.6.3 (R Core Team, 2020) and code to reproduce SDM analyses are available on GitLab (DOI: https://doi.org/10.5066/P9YYKW1H) and data are available on Science Base (https://doi.org/10.5066/P9O7MC7M).

2.6. *Conserved lands*

We used the best model's projection of spadefoot occurrence in southern California to estimate the area of extant habitat that falls within 1) "protected areas" that currently have conservation protections (e.g., federal, state, or regional parks), 2) lands owned by the U.S. Department of Defense ("DoD lands"), and 3) "unprotected" spaces that currently have no conservation protections. We classified the continuous occupancy probability into discrete classes for this analysis because it enabled us to present a simple comparison of how much extant habitat for western spadefoots remains in protected areas, DoD lands, and unprotected lands. We classified the continuous prediction of spadefoot occupancy probability into four occupancy categories using natural breaks (Jenks, 1967) rounded to the nearest tenth: very low ($\psi = 0$–0.1), low (>0.1–0.3), medium (>0.3–0.5), and high probability of occurrence (>0.5–1.0). We compiled data on protected areas and DoD lands in southern California from the California Protected Areas Database (CPAD; www.CALands.org), spatial data on U.S. DoD lands in the study region, as well as records developed by the San Diego Monitoring and Management Program (SDMMP; www.sdmmp.com). We then overlaid protected areas and DoD lands (Fig. A1) onto the classified occupancy surface and extracted 1 km^2 grid cells within and outside of protected areas and DoD lands within each occupancy class. We calculated how much of the western spadefoots' current distribution is in protected areas and DoD lands. We also visually assessed where large tracts of putatively suitable habitat exist that are currently unprotected.

To evaluate the coverage of spadefoot habitat by regional conservation plans, we quantified the area within each occupancy class that fell within 1) an implemented conservation plan (NCCP or HCP) covering all areas within a region, 2) an implemented conservation plan that covers discrete linear or energy projects within a broader region (hereinafter a "discrete plan"), 3) an in-progress conservation plan, and 4) no conservation plan (Table A3, Fig. A2). Within areas covered by implemented or discrete conservation plans, we also assessed how much habitat had conservation protections.

3. Results

Western spadefoots were detected by pitfall trapping in 68 out of 376 surveyed 1 km^2 cells. Of these 68 1 km^2 cells with spadefoot detections, 63 were trapped in three or more years, 23 of which had a pattern of initial detection, followed by one or more years of non-

Table 1
Parameter estimates from the best integrated species distribution model for western spadefoot (*Spea hammondii*) occurrence in southern California, USA. CI = confidence interval, SE = standard error, PB = presence-background, SO = site-occupancy. Parameters were estimated by maximum likelihood using Eqs. 1–4.

					CI	
Model	Parameter	Description	Mean	SE	2.5%	97.5%
Occurrence	$\beta 0$	Intercept of occurrence probability	-2.44	0.41	-3.24	-1.64
	βsl	Slope (degrees)	-1.03	0.17	-1.36	-0.70
	βsl^2		-0.26	0.22	-0.69	0.17
	βel	Elevation (km)	-0.76	0.19	-1.13	-0.39
	βel^2		-0.40	0.20	-0.79	-0.01
	βsn	% Sand in the soil within 1000 m buffer	0.48	0.12	0.24	0.72
	βsn^2		-0.31	0.11	-0.53	-0.09
	βgs	Proportion of grassland/shrub within 1000 m	1.14	0.17	0.81	1.47
	βgs^2		-0.07	0.17	-0.40	0.26
	βeph	Distance to ephemeral stream	-1.51	0.73	-2.94	-0.08
	βvp	Distance to vernal pool or pond	-0.93	0.23	-1.38	-0.48
PB sampling bias	α_0	Intercept of presence-only probability	-2.80	0.20	-3.19	-2.41
	α_{urb}	Distance to urban center (km)	-0.22	0.15	-0.51	0.07
	α_{rd}	Distance to major road (km)	-0.18	0.11	-0.40	0.04
SO detection	γ_0	Intercept of detection probability	-1.48	0.11	-1.70	-1.26
	γ_{eff}	Trapping effort	0.49	0.07	0.35	0.63
	γ_{ppt}	Water year precipitation	-0.14	0.10	-0.34	0.06

detection, followed by a subsequent detection of western spadefoots (i.e, a 1,0,…,1 pattern). Also, 43 out of 68 cells had one or more years of trapping without detecting a western spadefoot before the first detection, indicating that non-detection at occupied sites was common.

The modern occurrence of western spadefoots in southern California was positively related to the amount of grassland or shrub/ scrub land cover surrounding a location, and positively related to the sandiness of the soil up to a peak (approximately 60% sand in the upper 50 cm of soil), after which occupancy probability plateaued or declined. Western spadefoots were more likely to occur at lower elevations, on flatter slopes, and near ephemeral bodies of water (Fig. 2). There was some evidence of sampling bias in the presence-only data, with western spadefoot records more likely to be reported near urban centers and major roads, albeit with 95% confidence intervals that overlapped zero for these parameters (Table 1, Fig. A3). The detection probability of western spadefoots in pitfall trap arrays was positively related to the trapping effort that year, with weaker support for a negative relationship with annual precipitation (Table 1, Fig. A3).

The integrated SDM performed best in the blocked cross-validation when landscape-scale covariates were characterized within a 1000 m buffer of spadefoot occurrences (according to both predictive log-likelihood and AUC), with 500 m and 2000 m buffers performing only slightly worse (Fig. 3). The predictive ability of the integrated SDM for withheld SO data generally increased as the weight given to SO data increased, but the predictive log-likelihood declined when SO data was weighted ≥ 0.9. The optimal weighting of each data source in the model likelihood was 0.85 for SO data compared to 0.15 for PB data according to predictive log-likelihood, whereas for AUC the optimal weighting was 0.95 for SO and 0.05 for PB data (Fig. 3). Results from the random cross-validation were similar, with a 1000 m buffer producing the best predictions, and an optimal data weighting of 0.8 or 0.85 for SO data according to both AUC and predictive log-likelihood (Fig. 3). Model discrimination was higher on training data (detection/non-detection data from the four blocks used to fit the model; AUC = 0.81) and in random cross-validation (mean AUC = 0.76) than blocked cross-validation

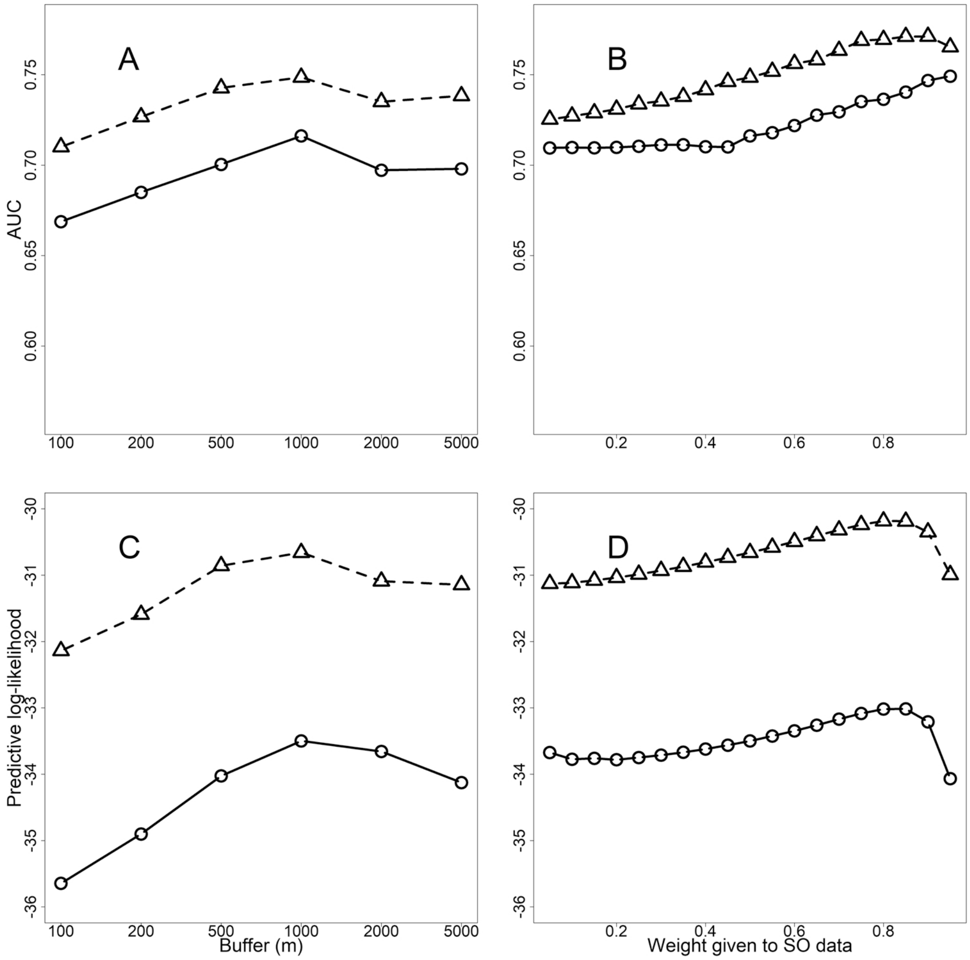

Fig. 3. Model predictive ability as a function of buffer distance for landscape covariates and weighting of site-occupancy (SO) data using blocked cross-validation. The top row (panels A and B) displays Area Under the Receiver Operating Curve (AUC) and the bottom row (C,D) displays the predictive log-likelihood. In both cases, higher values are better. The left column (A,C) displays model predictive ability vs. buffer distance, the right column (B,D) shows predictive ability vs. the weight given to SO data compared to presence-only data. The solid line with circles represents blocked cross-validation, the dashed line with triangles represents random cross-validation.

(mean AUC = 0.69), as expected. When predictions were evaluated on presence-only records from 2017 to 2020, the model performed well at discriminating recent western spadefoot occurrences from background points (AUC = 0.81).

The majority of remaining habitat with high occupancy probability for western spadefoots in southern California is in the southern half of the historical range (Fig. 4). The best integrated SDM predicts large regions with a high probability of spadefoot occurrence in western Riverside County, northwest and west central San Diego County, and southeastern Orange County. There is low probability of western spadefoot occurrence throughout most of the species' historical range in Los Angeles County, where low elevation habitats have been developed into urban and suburban land uses. In Ventura and San Bernardino counties, some small patches of high predicted spadefoot occurrence remain, but these regions appear isolated from the rest of the current distribution of the species (Fig. 4). The uncertainty in predicted western spadefoot occupancy probability was highest in western Riverside County and eastern San Diego County, in areas with high predicted probability of occupancy but few or no pitfall trapping arrays (Fig. A4).

Implemented and discrete conservation plans combine to cover most of the area predicted to have a medium or high probability of western spadefoot occurrence. Implemented conservation plans cover 46.8% of the area classified as medium probability of spadefoot occurrence and 44.1% of the area classified as high probability of spadefoot occurrence (Table 3; Figs. 5,6, A3). Discrete conservation plans also cover a large proportion of the areas classified as having a medium (35.6%) or high (49.1%) probability of spadefoot occurrence. Although implemented and discrete conservation plans ostensibly provide spatial coverage of most of the areas in southern California predicted to have medium to high probability of spadefoot occurrence, less than half of the total area in these two occupancy classes currently have protected status or are within DoD lands. Just 28.9% of all 1 km^2 cells classified as medium occupancy probability are currently protected and an additional 5.2% are on DoD land. Similarly, 24.7% of all high occupancy cells are in protected lands. Notably, an additional 17.4% of high occupancy probability cells are on DoD land, despite DoD land making up only 2.7% of the study region (Table 2). Three DoD bases in San Diego County with extant vernal pool complexes, Marine Corps Base Camp Pendleton, Fallbrook Naval Weapons Station, and Marine Corps Air Station Miramar (Fig. A1), cover most of the high occupancy western spadefoot habitat on DoD lands (Fig. A5).

Contiguous blocks of unprotected habitat with a high probability of spadefoot occurrence are found in central San Diego County (Fig. 6, A6). Likewise, unprotected areas with high predicted probability of spadefoot occurrence are found in western Riverside County (Fig. 6, A6). Fewer areas of highly suitable but unprotected land are present elsewhere in the historical range of the western

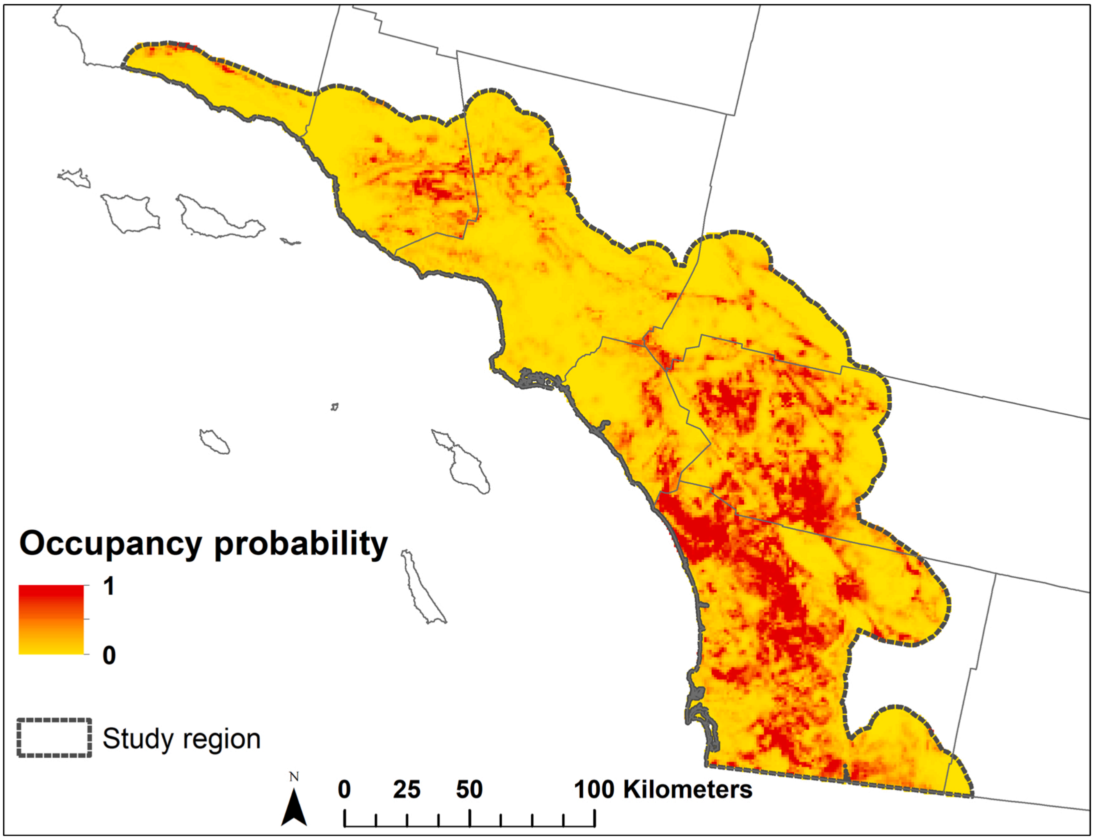

Fig. 4. Predicted probability of occurrence, ψ(s) of western spadefoots (*Spea hammondii*) in southern California. Warmer colors indicate a higher probability of western spadefoot occurrence. The prediction is from the best performing integrated SDM projected onto 2016 National Land Cover Data. For some regions, including the Los Angeles Basin, soil data were not available, and the model was projected assuming the % sand in the soil was equal to the average for the study region. The study region is the historical range of western spadefoots buffered by 10 km.

Table 3
Proportion of the western spadefoot (*Spea hammondii*) range in southern California that is covered by 1) an implemented conservation plan, an in-progress conservation plan, an implemented conservation plan covering discrete linear or energy projects within a wider region (“Discrete”), or no conservation plan (“None”) within each occupancy probability class. The “Total Area” column presents the total area in km^2 of that occupancy class.

	Conservation plan status				Total Area
Occupancy class	Implemented	In-progress	Discrete	None	(km^2)
Very low	0.20	0.14	0.15	0.51	17,841
Low	0.44	0.08	0.26	0.23	6434
Medium	0.47	0.06	0.36	0.12	2567
High	0.44	0.03	0.49	0.04	2072
Total	0.30	0.11	0.21	0.38	28,914

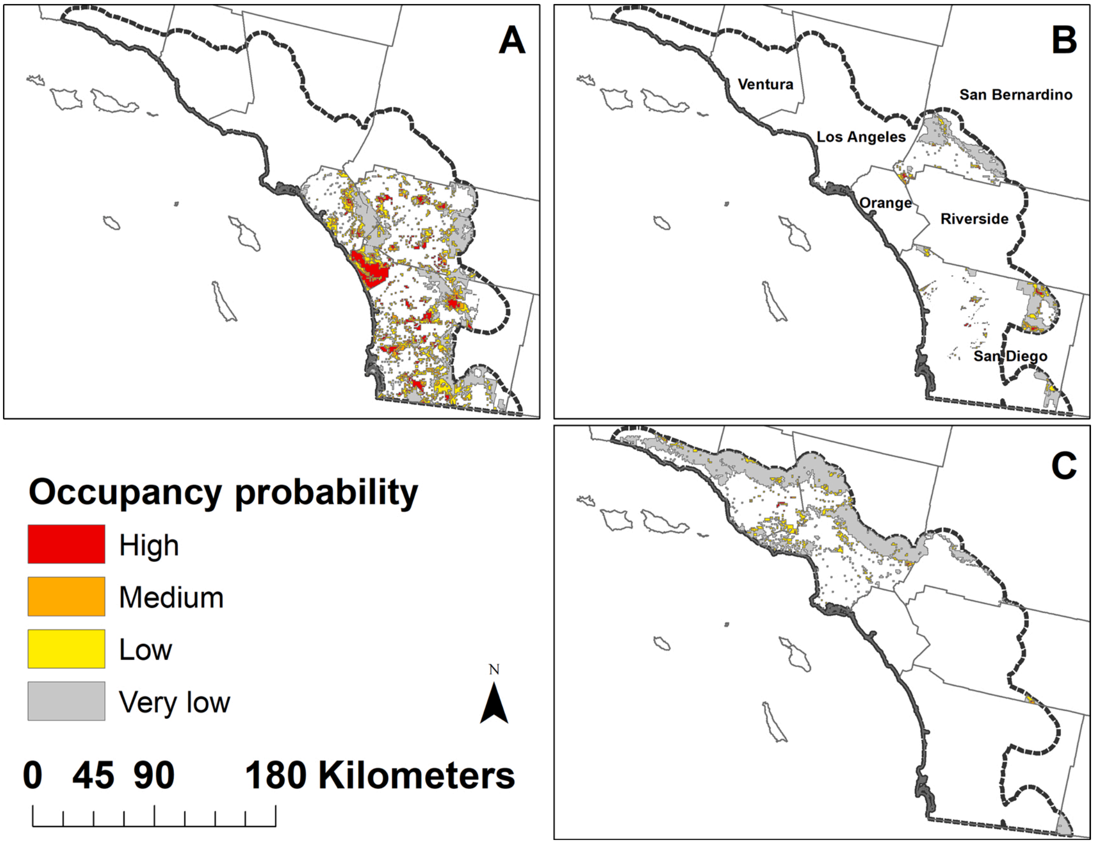

Fig. 5. Classification of spadefoot occupancy probability for areas in the southern range of the western spadefoot (*Spea hammondii*) that are currently U.S. Department of Defense lands or protected by local, state, or federal government or non-governmental organizations. Areas in panel A are within an implemented or discrete regional conservation plan, areas in panel B are within an in-progress regional conservation plan, and areas in panel C are not currently within a regional conservation plan. A very low occupancy classification corresponds to a predicted probability of spadefoot occurrence between 0 and 0.1; a low classification corresponds to a probability of spadefoot occurrence between 0.1 and 0.3; a medium classification corresponds to a probability of spadefoot occurrence between 0.3 and 0.5; a high classification corresponds to a probability of spadefoot occurrence ≥ 0.5.

spadefoot. Extreme southern Orange County has one contiguous patch of medium to highly suitable habitat, but few recent spadefoot records have been reported in this region (Fig. A6). Similarly, there are scattered and smaller patches of unprotected putatively suitable spadefoot habitat in Ventura County, and in western Los Angeles County along the Santa Clara River watershed (Fig. A6).

4. Discussion

The majority of remaining habitat for western spadefoots in southern California is found in the southern half of its historical range. The model projections in this study, with patchy areas with a high probability of spadefoot occupancy surrounded by larger expanses of unsuitable habitat within the historical range, confirm the decline evidenced in spatiotemporal patterns of western spadefoot

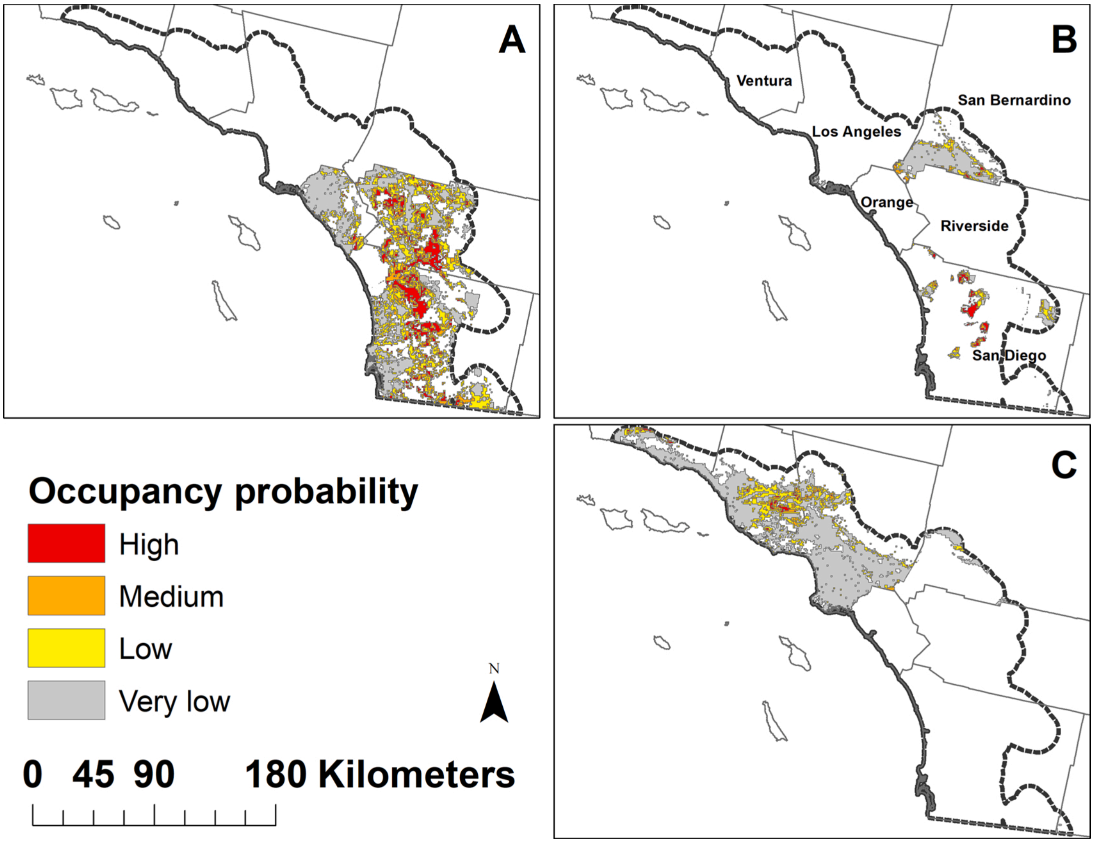

Fig. 6. Classification of spadefoot occupancy probability for areas in the southern range of the western spadefoot (*Spea hammondii*) that are currently unprotected by local, state, or federal government or non-governmental organizations. Areas in panel A are within an implemented or discrete regional conservation plan, areas in panel B are within an in-progress regional conservation plan, and areas in panel C are not currently within a regional conservation plan. A very low occupancy classification corresponds to a predicted probability of spadefoot occurrence between 0 and 0.1; a low classification corresponds to a probability of spadefoot occurrence between 0.1 and 0.3; a medium classification corresponds to a probability of spadefoot occurrence between 0.3 and 0.5; a high classification corresponds to a probability of spadefoot occurrence ≥ 0.5.

Table 2
Proportion of the western spadefoot (*Spea hammondii*) range in southern California that is in protected areas, on U.S. Department of Defense (DoD) lands, or not currently protected, by occupancy probability class. Occupancy class is based on predicted probability of occupancy from the integrated SDM. Protected areas are based on data from the California Protected Areas Database (www.CALands.org) and the San Diego Monitoring and Management Program (www.sdmmp.com). Total area is the area in square kilometers that falls within that occupancy class within our defined study area.

Occupancy class	Protected areas	DoD lands	Unprotected	Total Area (km^2)
Very low	0.43	0.01	0.56	17,862
Low	0.35	0.02	0.63	6445
Medium	0.29	0.05	0.66	2568
High	0.25	0.17	0.58	2073

observations in this region (Jennings and Hayes, 1994; Thomson et al., 2016). The occurrence of western spadefoots was primarily related to the distribution of open canopy grassland or shrub/scrub habitat and the proximity to suitable breeding habitat including ephemeral streams and vernal pools. Summarizing the amount of grassland/shrub land cover and the sandiness of the soil within a 1000 m buffer of spadefoot occurrences resulted in the best performing models, with 500–2000 m buffers also performing well. This finding highlights the value and extent of “core” terrestrial habitat surrounding breeding pools for western spadefoots (Halstead et al., 2021). The spatial extent at which terrestrial habitat influences western spadefoot occurrence is unsurprising given that adults spend the majority of the year aestivating underground and can move hundreds of meters from breeding sites to their burrows (Baumberger et al., 2019; Halstead et al., 2021). The importance of the landscape surrounding breeding sites has been documented for many pond-breeding amphibians (e.g., Gibbs, 1998, Trenham and Shaffer, 2005). Habitat fragmentation might have particularly acute effects in species with life cycles that require annual migrations between breeding and non-breeding habitat (Becker et al., 2007) and those that spend a longer time in the non-breeding habitat (Kadoya et al., 2008). Grassland and shrubland habitat greatly decreased in area in California in the late 20th century (Sleeter et al., 2011), and this habitat loss and fragmentation is likely to have contributed to the reduced distribution of the western spadefoot in southern California.

Comparing the modeled distribution of western spadefoot occupancy to the spatial coverage of regional conservation plans reveals both apparent positive outcomes and shortcomings for conservation planning. The vast majority of areas predicted to have a high probability of western spadefoot occupancy fall within the footprint of regional conservation plans implemented during the past 25 years, whereas little high occupancy habitat exists in areas lacking a conservation plan. Still, within the regions covered by an implemented or discrete conservation plan, 61% of the habitat classified as having a medium or high probability of western spadefoot occurrence is not currently protected (or within DoD land). This highlights that the existence of a conservation plan on paper does not guarantee protection of habitat for all species that occur within the geographic footprint for that plan. Habitat within a conservation plan area might not be protected yet because the planned conservation network is not completed (i.e., not all land has been acquired) and in the meantime the habitat is at risk of disturbance and degradation from activities like off-highway vehicle use. Similarly, because extant habitat on DoD land is not necessarily protected and managed for conservation goals, a change in mission needs on a given DoD base could lead to changes to existing spadefoot habitat. Even for areas with a high probability of western spadefoot occupancy that do have conservation protections, we cannot conclude from our SDM results alone whether those conservation protections are working to sustain healthy populations of this species. Evaluating the effectiveness of conservation protections for local and meta-population viability will require long-term data on the demographic vital rates and genetic structure (e.g., Neal et al., 2020) of western spadefoot populations.

Given the reduced range of the western spadefoot in southern California, protecting remaining habitat, even within existing conservation plans, could be vital for ensuring this species persists in this heavily fragmented landscape. Our analysis shows that some unprotected but potentially high-quality habitat exists in parts of northern and central San Diego County for which regional conservation plans are in progress. Only small patches of habitat with a high probability of spadefoot occupancy exist outside of regions with a conservation plan at any stage, largely in the northwestern part of the historical range, in eastern Ventura County and northern Los Angeles County. Some of the areas predicted to have a high probability of occurrence do not have recent records of western spadefoot presence, possibly due to accessibility of private lands, and would be good targets for future surveys. For example, central San Diego County east and north of the city of Escondido, south-central San Diego County just north of the border with Mexico, and western Riverside County in the hills east of the city of Temecula. These potentially suitable sites could be considered for mitigative strategies to improve the habitat through breeding site creation (Baumberger et al., 2020) thus enhancing the regional population resiliency (Neal et al., 2020).

To best leverage the available data on the occurrence of western spadefoots in southern California, we fit a SDM that integrated spatially limited site-occupancy data with more widespread presence-only data into a joint likelihood weighted towards the higher-quality occupancy data (Fletcher et al., 2019; Koshkina et al., 2017). In fitting this model to our data, we assumed that the occupancy of western spadefoots within 1 km cells was fixed during the period in which they were sampled (the "closure assumption") and used the estimated relationships between environmental predictors (including contemporary land cover) and spadefoot occurrence to project this species' distribution onto 2016 land cover. Although the closure assumption is likely to be violated in reality, we believed it was a necessary trade-off in order to integrate multiple data sources to produce the most informative model about areas potentially occupied by western spadefoots. Violation of the closure assumption can lead to biased estimates of ψ (Rota et al., 2009); however, some authors have advocated for a broader definition of occupancy that includes species presence at some point during the relevant time period (Latif et al., 2016). This more inclusive definition of occupancy was appropriate for our goal of identifying areas potentially occupied by western spadefoots on the modern landscape. The implementation of regional conservation plans could have resulted in changes in occupancy during the sampling period if the amount of habitat for western spadefoots increased as a result. These conservation plans primarily protected remaining open spaces and native habitats rather than increasing the amount of habitat for western spadefoots, and therefore would be expected to stabilize rather than increase occupancy. Despite the amount of land cover change that took place in southern California in the late 20th century, the grassland and shrub/scrub cover in our study area did not change much from 2001 to 2016. The area of grassland or shrub/scrub land cover within 1000 m of pitfall traps exhibited $<$ 10% change for 354 out of 376 of 1 km cells (94.1%), which indicates that our static modeling approach likely did not obscure dramatic changes in western spadefoot occupancy during our study period. In contrast, grassland and shrubland habitats are the two natural land cover types predicted to exhibit the largest proportional declines in California in the 21st century, with southern California projected to exhibit the highest rates of future urbanization (Sleeter et al., 2017).

As land cover change continues in southern California, capturing the dynamics of western spadefoot occupancy will be essential for future conservation planning and management. Future work could expand upon our approach by explicitly modeling the dynamics of western spadefoot occupancy in response to changing land cover and climatic conditions. For example, a relevant question might be how the probability of spadefoot extirpation changes as the amount of grassland and shrub land cover surrounding breeding habitat changes. Dynamic occupancy and species distribution models can explicitly model the processes that produce changes in species' ranges over time (Evans et al., 2016; Royle and Kéry, 2007). A dynamic modeling approach was not possible with the data available for this study, because the SO data alone did not capture the extent of western spadefoots in southern California, and the presence-only data for western spadefoots were not consistently distributed in space and time. Therefore, if we attempted to model the change in spadefoot occurrence by fitting integrated SDMs to data from multiple time periods, any apparent changes in western spadefoot distribution would likely be an artifact of spatiotemporal patterns in sampling and not true range dynamics. Given the potential synergy between future climate change (Diffenbaugh et al., 2015) and land cover change (Sleeter et al., 2017) in southern California, projecting future western spadefoot viability in the long term will require a model that captures the interaction between the dynamic processes of land cover change, climate change, and population extirpation and colonization.

4.1. Summary and conclusions

Our study integrated multiple data sources to project the current distribution of western spadefoots in southern California to model where this species persists in a highly altered landscape and how much of the remaining habitat has conservation protections. Suitable habitat for western spadefoots in southern California is now largely restricted to the southern half of its historical range, where regional conservation plans have been implemented. Within regions covered by regional conservation plans, some large patches of spadefoot habitat are currently protected by federal, state, local, or non-governmental organizations, or owned by the U.S. Department of Defense. However, even within areas covered by conservation plans, the majority of habitat with a medium to high probability of western spadefoot occupancy lacks any formal conservation protections. Conservation ownership for such parcels can be lacking because although the plan is approved, the conservation network of protected lands is not yet completed. Further, it remains unknown how well conservation protections ensure the viability of extant populations within the plans. Our model projections and comparison of the distribution of remaining habitat and protected lands provides valuable information for decision-makers who must assess the conservation status of the western spadefoot in southern California. We identified additional unprotected areas that are predicted to have high probability of spadefoot occurrence and occur within areas covered by conservation plans that could be targets for conservation acquisitions in the future. Given the loss of grasslands and shrublands in California in the late 20th century (Sleeter et al., 2011) and the projected continuing expansion of human-dominated land uses as the state's population grows (Sleeter et al., 2017), implementation of in-progress land use plans, the protection of remaining habitat, and active management where conservation plans are in effect could be vital for the continued persistence of western spadefoots in southern California.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank C. Rochester, C. Brown and J. Mulder for compiling and conducting the QA/QC for records of western spadefoot occurrence. We thank K. Baumberger, T. Toure, E. Gallegos, A. Backlin, S. Hathaway, E. Ervin, D. Stokes, R. Hamilton, D. Erickson, S. Riley, C. Hitchcock, K. Delaney, numerous biological technicians, and citizen scientists for their work collecting data on spadefoot occurrence, and to Marine Corps Base Camp Pendleton for sharing occurrence data. This work was supported by funding from the U.S. Geological Survey's Western Ecological Research Center and Amphibian Research and Monitoring Initiative, the Nature Conservancy, San Diego Association of Governments, and the U.S. Fish and Wildlife Service. All field research was performed under the Scientific Collecting Permit SC-838 from the California Department of Fish and Wildlife. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is contribution number 823 of the U.S. Geological Survey Amphibian Research and Monitoring Initiative (ARMI).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01944.

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