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Drought-related monitoring, habitat-use, and prioritization of conservation sites for Tricolored Blackbirds

By

National Audubon Society

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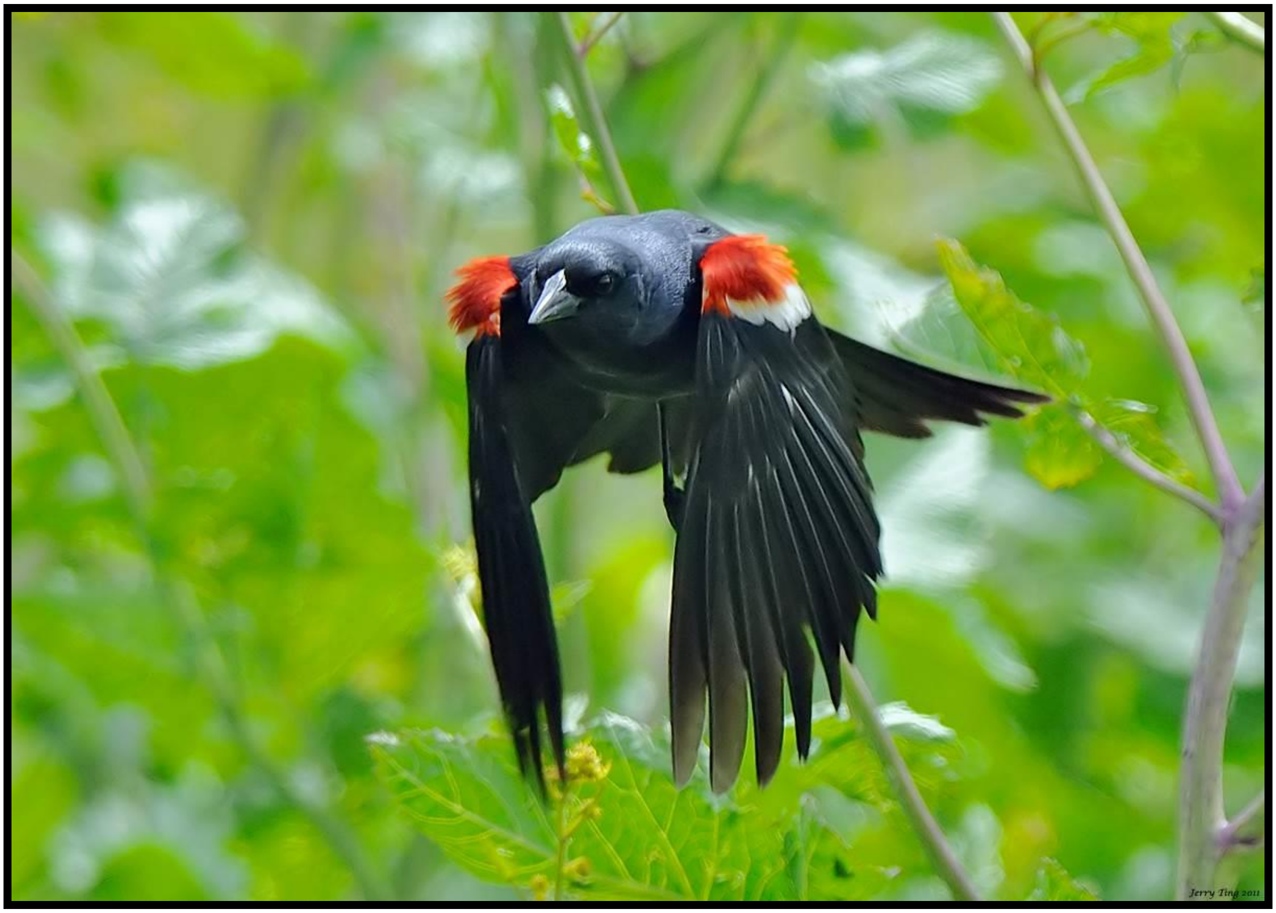

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1 EXECUTIVE SUMMARY

Colonial nesting birds are highly vulnerable to extinction. The Tricolored Blackbird (*Agelaius tricolor*, TRBL hereafter) is a colonial nesting species largely endemic to California that has experienced dramatic population declines in the 20th century. We used the triennial Tricolored Blackbird (TRBL) surveys from 2008, 2011, and 2014 along with eBird checklist and environmental data from the same time periods to model both the probability of occurrence and relative abundance of TRBL colonies. Environmental datasets included land cover, surface water, vegetation condition, precipitation and frequency of adjacent dairies. Occurrence and abundance models were used in combination to characterize the landscape composition around known early breeding season colony sites and to map core habitats across four ecoregions in California. Simulated landcover changes were used to identify potential habitat under restoration scenarios. Finally, we explored the impact of landcover change (in relation to prolonged drought) on colony abundance across the three triennial surveys with linear mixed-effects models.

The proportion of alfalfa and grasslands within 5 km of colonies, and surface water within 500 m were identified as predictors of TRBL foraging habitat. Year and ecoregion were also important. Landcover change across years had both positive and negative effects on TRBL colonies. Across the study region, grasslands declined over time, surface water decreased in dry years, and alfalfa increased in the driest years. Surface water declined over time in unoccupied colonies but remained stable in occupied colonies, confirming that permanent surface water was a critical feature of persistent TRBL colonies. Finally, average percent cover of nearly all land cover types, frequency of dairies, and median NDVI were all higher in known colony sites than elsewhere. This highlighted the importance of conserving both current and historic TRBL colony sites for providing key habitat characteristics of limited availability elsewhere in the state.

We mapped early breeding season TRBL foraging habitat across the study area, identifying over six million acres of core habitat in this region. The majority was concentrated in the Central Valley and surrounding foothills. Protection of these lands, through acquisition and easements is a key conservation strategy for TRBL. Simulations also identified potential habitat where increased cover of alfalfa, grassland, or surface water would increase habitat availability. Engaging with landowners to expand the acreages of these important landcover types is a possible strategy for TRBL habitat restoration. The vast majority (93.5%) of TRBL core habitat is private land. Therefore, efforts to increase the long-term stability of the TRBL population will require engagement with landowners to inform choices regarding crop selection, land conversion, and surface water management.

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2 INTRODUCTION

Colonial nesting birds for which a few colonies comprise a significant proportion of the total population are particularly vulnerable to population declines and extinction (Cook and Toft 2005). The Tricolored Blackbird (*Agelaius tricolor*, TRBL hereafter) is a colonial nesting species largely endemic to California (Meese et al. 2014). The species experienced historical declines of total population size of 89% from the 1930's to the 1980's (Meese et al. 2014), and average colony size declined by 60% between the 1930's and 1970 (Graves et al. 2013). Statewide surveys found an initial total count of 395,000 birds in 2008 followed by a decline to 259,000 in 2011 and only 145,000 in 2014 (Meese 2014), which represents the smallest count ever recorded. Work by Meese (2013) also found that TRBL had unusually low breeding success between 2006 and 2011, which presumably contributed to declines in abundance. The extinction vulnerability of the species is worsened by the fact that about half of the population typically occurs in a small number of large colonies in silage fields during the initial nesting attempt. On 8 January 2016 the species was given statewide protection as a candidate species for listing under the California Endangered Species Act (CESA). Also on 3 February 2015 the Center for Biological Diversity petitioned U.S. Fish and Wildlife Service (USFWS) for federal listing of the species, and on 18 September 2015 the USFWS initiated a status review for the species.

Breeding TRBL colony sites must have appropriate nesting substrate, access to open water, and suitable nearby foraging habitat providing adequate arthropod prey and seeds (Meese et al. 2014). Increasing the availability of suitable breeding sites outside of agricultural fields, where annual recruitment for a colony can be lost due to early harvests, is a key conservation objective for the species (Cook and Toft 2005). Historically, TRBLs nested in the large wetland complexes of cattails and bulrushes that occurred throughout California's Central Valley (Meese et al. 2014, Graves et al. 2013, Cook and Toft 2005). However, much of these wetlands have been converted to agriculture; estimated net loss was 95% from 1939 to the mid-1980s (Frayer et al. 1989). Today, breeding TRBLs are found in native stinging nettle and thistle, exotic blackberry, cultivated fields of triticale grain and remaining wetlands (Graves et al. 2013, Holyoak et al. 2014). Both occupancy and reproductive success varies among these habitat types annually such that permanent nesting habitats (i.e., stinging nettle and blackberry), despite their lower annual productivity, may be more important for the species than cultivated fields (Holyoak et al. 2014), even though the latter host the largest single-year colonies (Kyle and Kelsey 2011).

Recent research has focused on assessing overall population trends of TRBL (Graves et al. 2013) as well as quantifying the relative productivity in specific nesting habitat types (Holyoak et al. 2014). There has been less work looking at factors behind year-to-year and among-site variation in breeding population sizes, site occupancy and reproductive success. Year to year variation in either weather, especially rainfall, and habitat availability could be important. Plantings of crops such as triticale are expected to vary from year to year, which could control the amount and distribution of a key breeding habitat. Both Holyoak et al. (2014) and Meese (2013) also suggest that landscape composition may be an important determinant of breeding success. Quantifying the landscape-scale factors influencing breeding abundance is critical for focusing conservation and restoration activities towards those sites able to support significant and stable populations through time. Furthermore, impacts of recent drought conditions throughout California captured in landscape-scale changes in crop coverage or surface water (Soulard and Wilson 2015) may contribute to recent TRBL population declines.

Here, we identify the preferred landscape composition utilized by nesting TRBLs, look for the potential impacts of drought on TRBL abundance, and generate maps prioritizing areas for restoration and/or habitat management, to be shared with the TRBL Working Group and state conservation officers. We followed a three-pronged approach, first identifying landscape conditions critical to TRBL presence and abundance; then looking for signals that land-use changes during the study period have impacted TRBL foraging habitat or abundance; and finally mapping core habitat and areas for potential restoration.

3 LANDSCAPE MEASURES OF FORAGING HABITAT

3.1 LANDSCAPE MODELING

We first sought to identify landscape composition conditions critical to TRBL abundance in nesting colonies through the development of an abundance model. Our goal was to identify suitable composition of breeding substrate, forage, and water based on statistical models of TRBL presence and abundance at breeding sites. The analysis focused on conditions surrounding known nesting sites, including those found in wetlands and upland habitats, likely to be the focus of conservation efforts (Holyoak et al. 2014). Audubon used the results of state-wide TRBL surveys from 2008, 2011, and 2014. Because of the timing of the survey in April, this captures nesting sites from the first breeding of the year primarily in the foothills of the Sierra Nevada and San Joaquin Valley. Spatial data layers included annual crop data (from CropScape) as well as locations of dairy farms and surface water (including wetlands). We calculated landscape metrics such as the number of dairies and the proportion of certain foraging crops within a biologically meaningful distance of each colony (5-km or 500-m; see *2.2 Data Preparation* below). Audubon then built statistical models identifying key landscape conditions for nesting sites. In the following sections, we describe how these models were then used to identify criteria for site suitability across the region.

3.2 DATA PREPARATION

Audubon staff met with collaborators from UC-Davis to identify key datasets including: the triennial surveys (2008, 2011, and 2014), classified crop cover (CropScape), surface water and wetlands, vegetation condition (NDVI), locations of dairies, and fall to spring precipitation. For foraging habitat and surface water, the proportion of these land types within the foraging distance (see below) was identified as the most suitable summary statistic given expert knowledge of foraging behavior. Follow-up conversations occurred identifying crop types that serve as foraging habitat, and exploring different sources of surface water data and vegetation condition data.

We spoke with UC-Davis staff as well as conducted a literature search to define the appropriate spatial extent at which to summarize environmental data. Audubon chose 5-km as the foraging distance buffer based on several studies, including unpublished data from UC Davis (90th percentile = 4.5-km); Orians 1961 (5-km); and other historic data such as Crase and DeHaven 1977 (1.5 km and up to 6 km), and Hamilton and Meese 2006 (9 km). We summarized surface water at 500 m (Hamilton 2004).

The environmental datasets were assembled as continuous, 510-m resolution grids for each environmental variable covering the entire state. We selected 510 m because it was a multiple of the underlying, 30m-resolution gridded land cover dataset. Values within each grid cell represented features occurring within a 5-km radius and were generated with a moving window analysis on the original datasets. Further details provided below. In addition to the triennial surveys, eBird data through 2016 (Sullivan et al. 2009) were extracted statewide for the surveyed time periods. These were used to augment available spatial data for the occurrence model. We were interested in habitat around known colonies, which requires detection of nesting behavior in addition to presence. Therefore, eBird data was only used to augment data on colony absence by including only complete checklists where TRBL were not recorded. For all datasets, we assigned environmental data using the nearest grid cell in the state-wide gridded datasets. Data processing was completed in ArcGIS (ESRI) using off-the-shelf geoprocessing tools such as focal statistics and intersect; and gdal_grid (Open Source Geospatial Foundation).

The summarized environmental dataset was examined for accuracy using a randomly selected 1% of the complete dataset. Summaries of crop cover, surface water, NDVI, and precipitation were checked by comparing values calculated manually with outputs from geoprocessing scripts. Addresses of the dairy locations were visually checked against Google Earth to assess whether evidence of dairy operations occurred within 2-km of the recorded address. Accuracy of the triennial survey datasets was ensured by UC-Davis.

3.2.1 Foraging Crops

All the data on crops planted in 2008, 2011, and 2014 in California were downloaded from CropScape (USDA National Agricultural Statistics Service Cropland Data Layer 2016). CropScape was the most suitable data for identifying foraging crops in the selected years because it is an annual mapping product with coverage across the study area. The crops were organized into general categories: nesting substrates, foraging substrates, flower, tree, fruit and vegetable, seed, land, and water. Audubon discussed relevant foraging crop types with local experts and identified those commonly associated with TRBL: grass/pasture, rice, alfalfa, sunflower, and other hay/non alfalfa. For each, the proportion of coverage within 5-km of each grid cell centroid was calculated.

3.2.2 Dairies

Addresses of all dairies in California were provided by California Department of Food and Agriculture (California Department of Food and Agriculture 2014). Audubon staff manually converted these data from PDF documents to an Excel spreadsheet. Addresses were then geocoded with ArcGIS 10.3. The number of dairies was summed within a 5-km buffer of each grid cell centroid.

3.2.3 Precipitation

Monthly precipitation datasets (4-km resolution, October to April) for the years 2007-08, 2010-11, and 2013-14 were downloaded from PRISM Climate Group (PRISM Climate Group 2015). Audubon summed months to account for an entire water year of rainfall. Summed precipitation rasters were sampled at grid cell centroids.

3.2.4 Vegetation Condition (NDVI)

MOD13Q1 Normalized Difference Vegetation Index (NDVI) datasets for the years 2008, 2011, and 2014 were downloaded from U.S. Geological Survey MODIS Reprojection Tool Web Interface (USGS 2010). MOD13Q1 data had a 16-day interval with 250-m resolution. Audubon selected the image dates most closely aligned with triennial surveys and calculated the median NDVI within 5-km of each grid cell centroid.

3.2.5 Surface Water

The surface water data included Point Blue Conservation Science's surface water dataset (Reiter et al. 2015) and USFWS National Wetlands Inventory (NWI) (USFWS 2016). Freshwater Emergent Wetland and Estuarine and Marine Wetland were selected from the NWI. The two wetland datasets were merged using a union, and we calculated the proportion of surface water within 500 m of each grid cell centroid.

3.3 STATISTICAL MODELS

In order to identify the landscape composition utilized by nesting TRBLs, we developed abundance models to identify relationships with the environmental variables described above. However, because TRBL are a strongly colonial species, the abundance distribution was highly skewed, with many zero or low counts and a few very large counts. This makes modeling abundance relationships with traditional parametric models difficult (Martin et al. 2005). Therefore, we instead used a hierarchical "hurdle model" approach, in which we separately fit a presence-absence model that estimates probability of TRBL occurrence, and an abundance model that estimates abundance only where TRBL occurred (Wenger and Freeman 2008, Oppel et al. 2012).

We modeled TRBL presence and abundance relationships using boosted regression trees (BRTs), a machine learning approach that is ideal for modeling complex curvilinear relationships with multiple, and often highly correlated, environmental variables (Elith et al. 2008). Models were fit using packages *dismo* (Hijmans et al. 2015) and *gbm* (Ridgeway 2015) in R version 3.3.2 (R Core Team 2016). The response variables were presence/absence for the presence model, and log-transformed count for the abundance model. Presence/absence points were based on both triennials surveys and eBird sampling locations. Log-transformed counts were used to meet the assumption of normally-distributed data when using the Gaussian distribution.

BRT models use three parameters—learning rate, bag fraction, and tree complexity—to shrink the number of terms in the final model and thus avoid overfitting. Learning rate shrinks the contribution of each tree in the boosted model, bag fraction specifies the proportion of data to be selected from the training set at each step, and tree complexity determines the number of nodes and, consequently, level of interactions between predictors. We iteratively tuned these parameters to optimize model fit while ensuring a minimum of 1,000 trees using default parameter ranges recommended by Elith et al. (2008): learning rate 0.0001–0.1, bag fraction 0.55–0.75, and tree complexity 1–3. At each step we used 10-fold cross-validated area under the curve (AUC) and residual deviance to select the optimal parameter value. Our presence model had the following parameters: learning rate of 0.005, a bag fraction of 0.55 and a tree complexity of 1. The abundance model had the following parameters: learning rate of 0.0005, a bag fraction of 0.55 and a tree complexity of 1.

Species distribution and habitat models such as these are susceptible to spatial autocorrelation, which can result in biased presence/abundance – environment relationships. To reduce spatial autocorrelation in the models, we used spatially stratified cross-validation by dividing the datasets into 10 bins by latitude and withholding one latitudinal bin for testing at each fold (Roberts et al. 2017). We tested for residual spatial autocorrelation in the final models using Moran's I, calculated in package *ape* (Paradis et al. 2004).

3.4 RESULTS

Model performance was best when using triennial survey data and eBird data from four level III ecoregions (EPA 2013). Therefore, we restricted the study area to the portion of California encompassed by the Central Valley, Southern California Mountains, and Central California Foothills and Coast Range ecoregions and thereby avoided extrapolating to areas with low colony occurrence in April (Fig. 1).

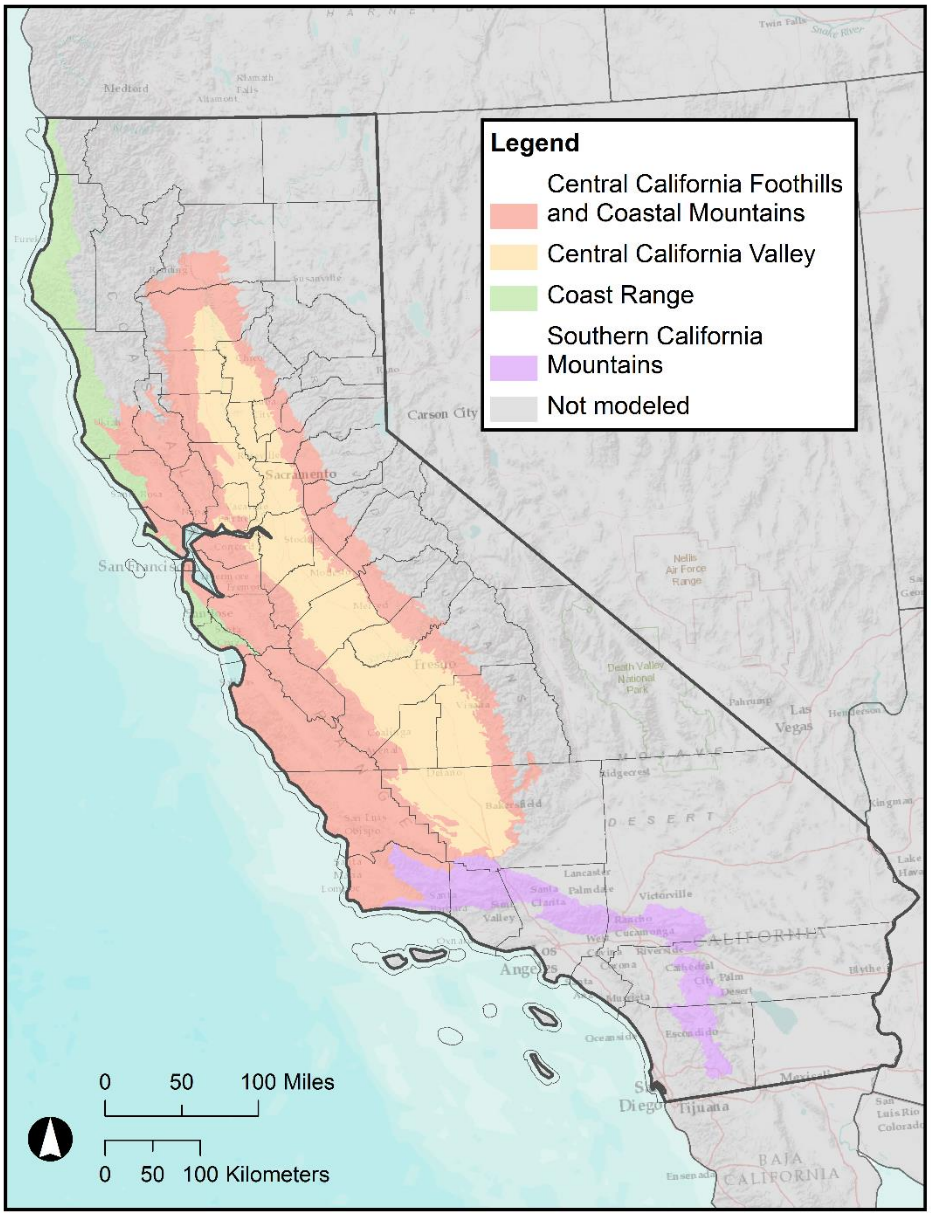


Figure 1. Study area and represented ecoregions. County and state boundaries included for reference.

3.4.1 Presence-Absence Model

The set of environmental covariates explained 31.9% of the deviance in the data for the presence-absence model, with a cross-validated correlation between observed and predicted presence of 0.36 and a cross-validated AUC of 0.90. The occurrence of TRBL was best predicted by year (explaining 40.1% of the model deviance), followed by proportion grassland cover (explaining 32.4% of the model deviance), proportion alfalfa (12.6%), ecoregion (5.8%), proportion of surface water (3.8%), number of dairies (2.1%), and proportion of rice (2.0%; Fig. 2).

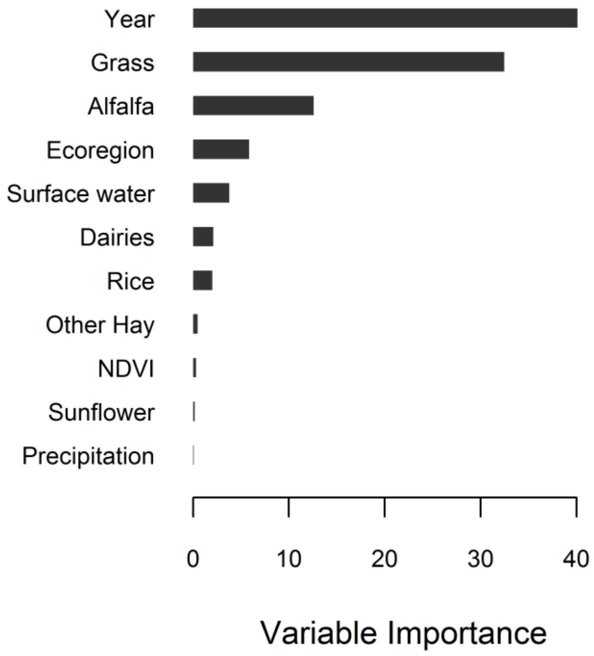
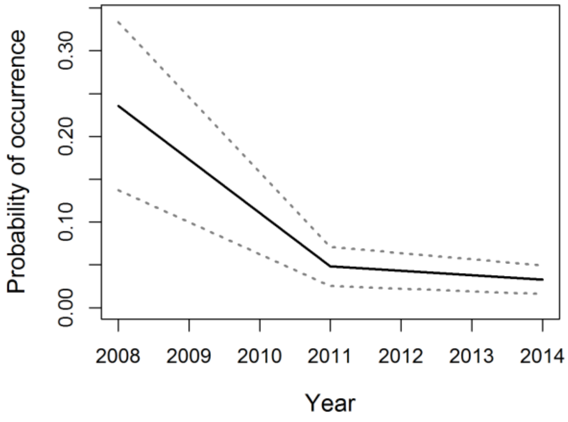
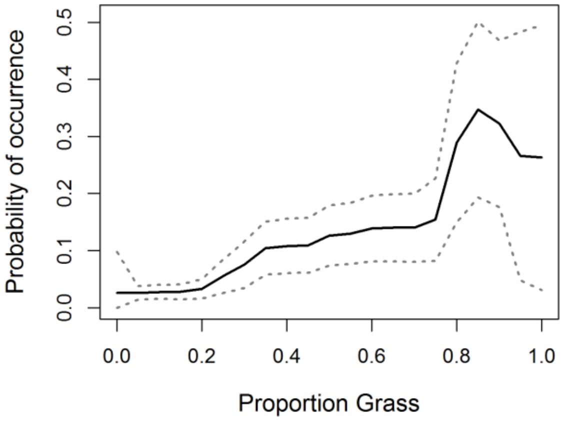
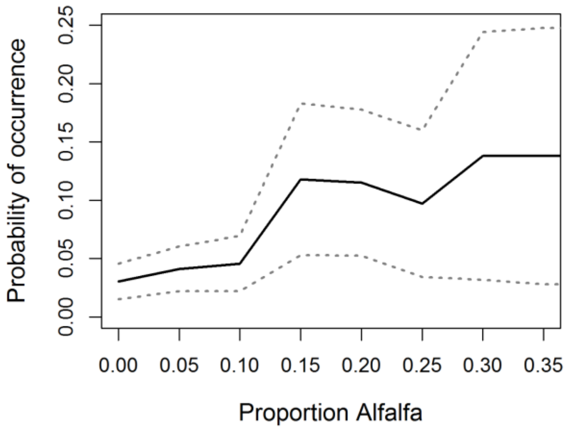
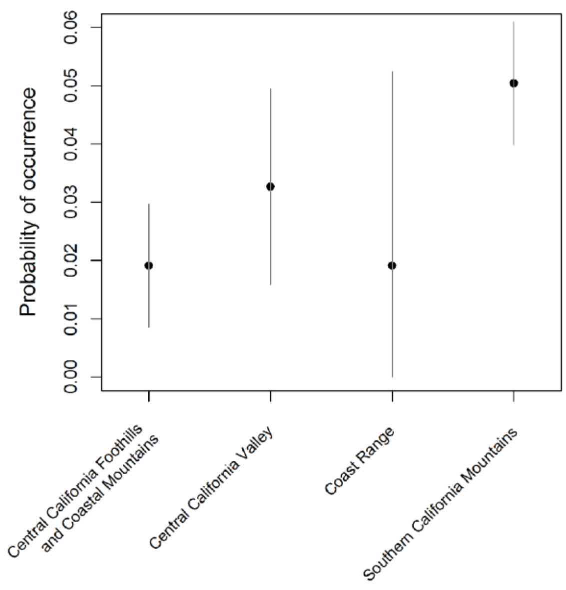


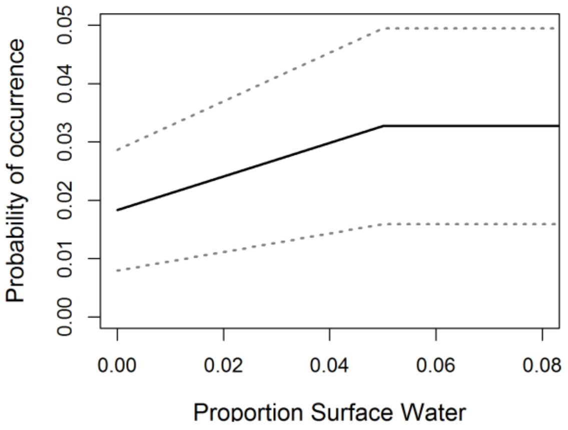
Figure 2. Variable importance scores, representing proportion of the model deviance explained by each covariate, for the TRBL presence-absence model.

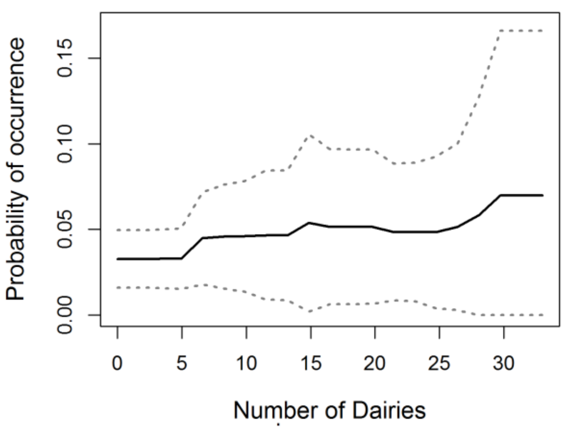

Probability of occurrence
0.00
0.10
0.20
0.30
2008
2009
2010
2011
2012
2013
2014
Year


Probability of occurrence
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.2
0.4
0.6
0.8
1.0
Proportion Grass


Probability of occurrence
0.00
0.05
0.10
0.15
0.20
0.25
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Proportion Alfalfa


Probability of occurrence
0.00
0.01
0.02
0.03
0.04
0.05
0.06
Central California Foothills and Coastal Mountains
Central California Valley
Coast Range
Southern California Mountains


Probability of occurrence
0.00
0.01
0.02
0.03
0.04
0.05
0.00
0.02
0.04
0.06
0.08
Proportion Surface Water


Probability of occurrence
0.00
0.05
0.10
0.15
0
5
10
15
20
25
30
Number of Dairies

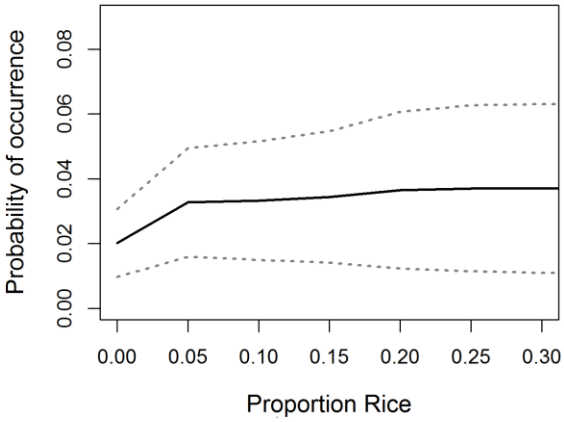


Figure 3. Response plots for the relationship between TRBL occurrence and environmental covariates explaining ≥1% of the model deviance in the model.

The probability of TRBL occurrence increased with proportion grassland, proportion alfalfa, number of dairies, and proportion rice (Fig. 3). Probability of presence also varied between ecoregions, with the highest probabilities in the Central Valley and Southern California Mountains, and lowest probabilities in the Central California Foothills and Coastal Mountains and Coast Range ecoregions. There was not substantial residual spatial autocorrelation remaining in the TRBL presence model (I = 0.016).

We identified a minimum threshold (0.02) below which habitats were classified as unsuitable for TRBL colony occurrence. Given that there were only 382 colony locations in the dataset, we selected a conservative threshold equivalent to a 5% omission error. Setting the threshold any lower resulted in an uninformative model that did not discriminate areas where TRBL colonies are less likely to be encountered. Higher thresholds, while producing lower errors of commission, reduced the area considered for abundance modeling considerably. Predicted probability of TRBL occurrence across California in April 2014, based on the environmental covariate relationships determined in the presence-absence model, is shown in Figure 4.

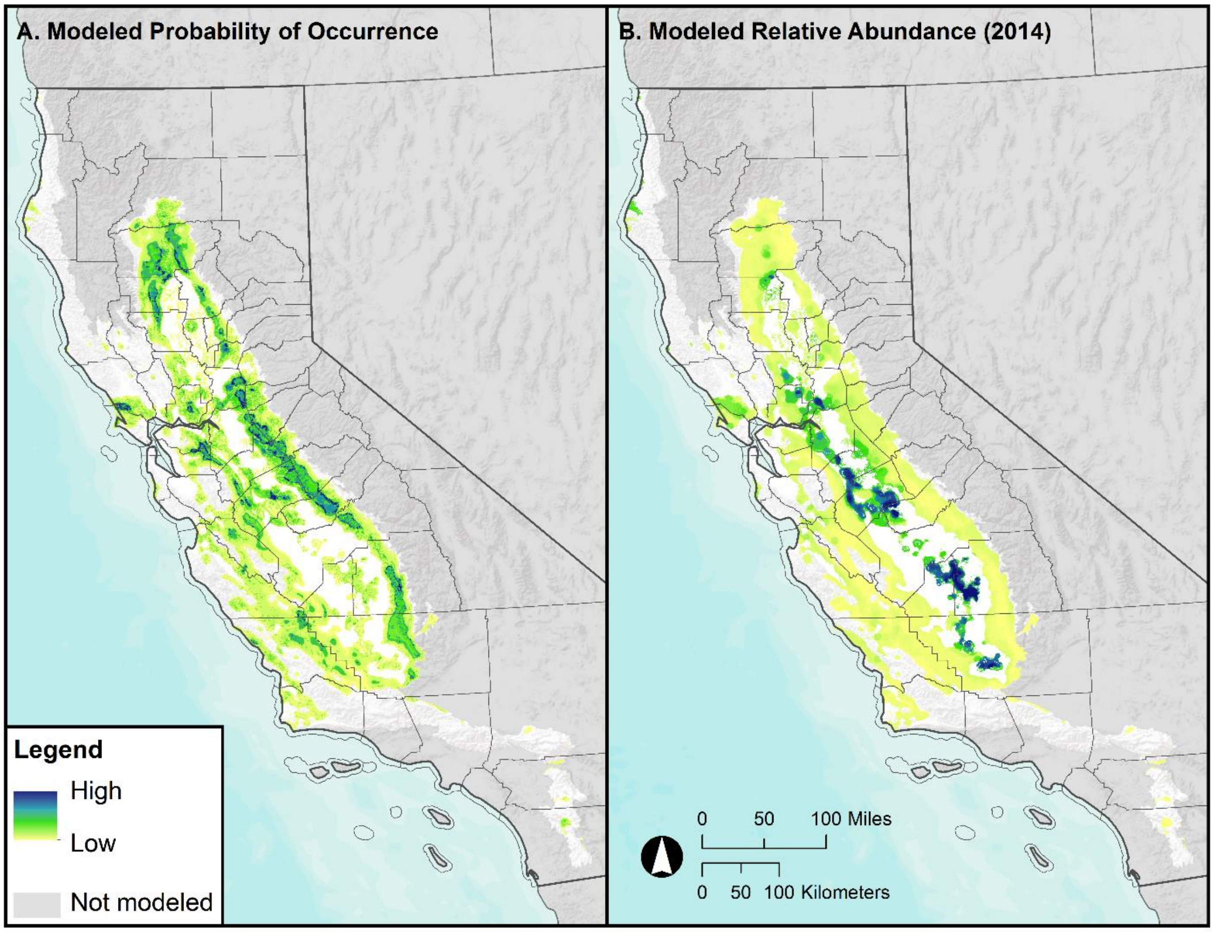


Figure 4. (A) Predicted probability of TRBL colony occurrence and (B) relative abundance across California in 2014, based on the environmental covariate relationships determined in the presence-absence and relative abundance models.

3.4.2 Relative Abundance Model

The set of environmental covariates explained 16.3% of the deviance in the data for the relative abundance model, with a cross-validated correlation between observed and predicted presence of 0.195. TRBL relative abundance was best predicted by proportion alfalfa (explaining 37.1% of the model deviance), followed by number of dairies (29.6%), ecoregion (12.5%), median NDVI (8.6%), precipitation (5.5%), proportion of grasslands (2.0%), proportion surface water (1.6%), and proportion of hay/other (1.2%; Fig. 5).

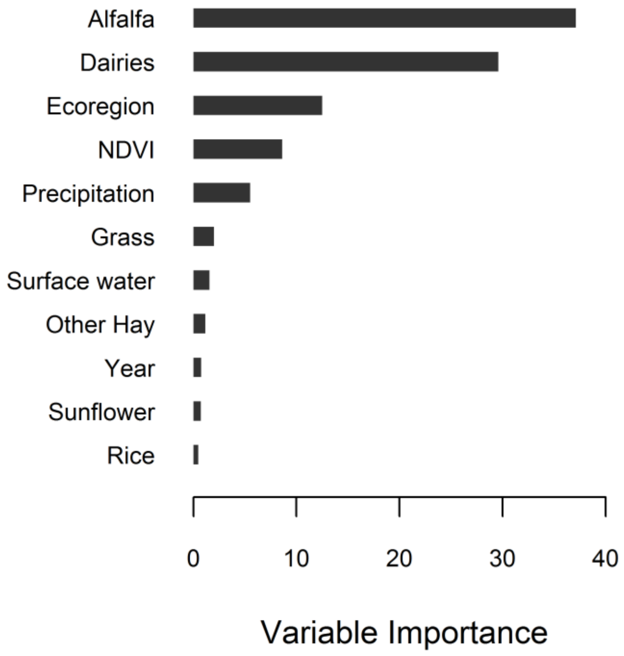
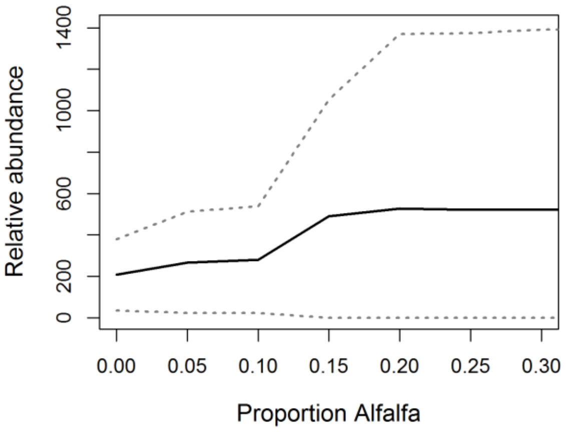
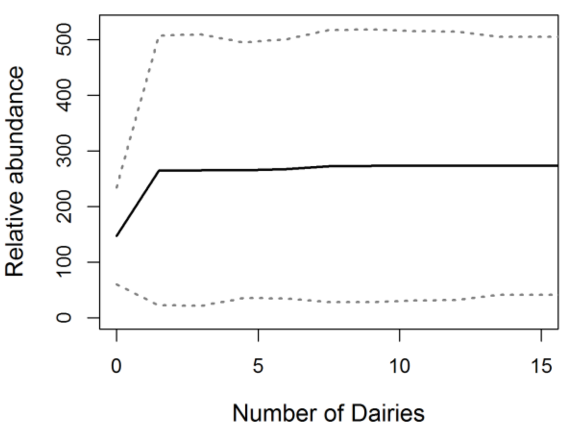
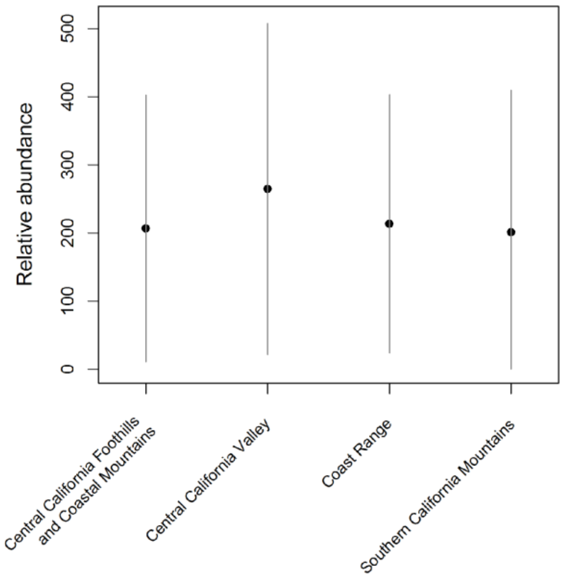


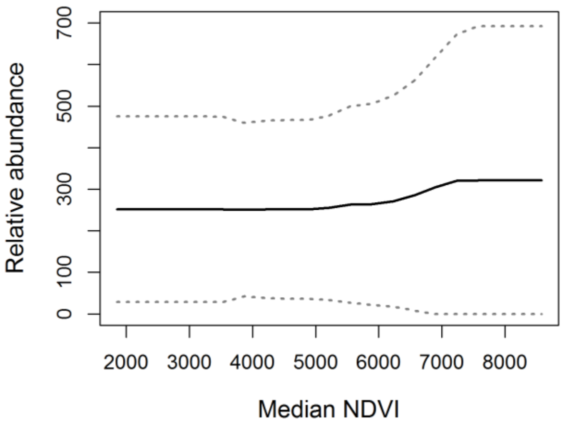
Figure 5. Variable importance scores, representing proportion of the model deviance explained by each covariate, for the TRBL relative abundance model.

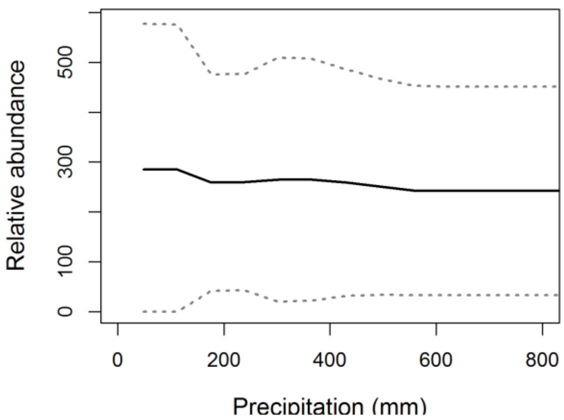
TRBL relative abundance increased with proportion of alfalfa, number of dairies, and median NDVI, and had relatively weak negative relationships with precipitation, proportion surface water, and proportion of grasslands (Fig. 6). Relative abundance also varied between ecoregions, with the highest predicted abundances in the Central Valley ecoregion. There was not substantial residual spatial autocorrelation remaining in the model (I = 0.058).

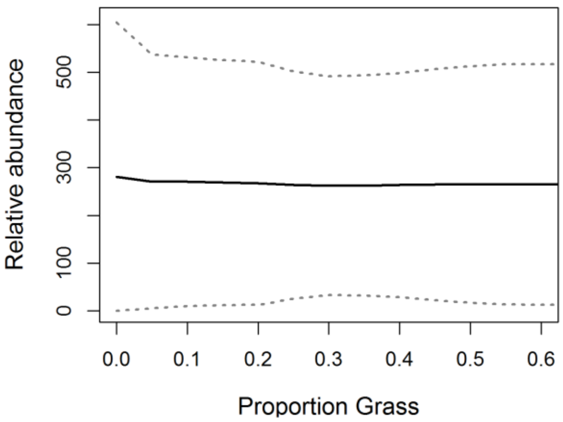

Relative abundance
0
200
600
1000
1400
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Proportion Alfalfa


Relative abundance
0
100
200
300
400
500
0
5
10
15
Number of Dairies


Relative abundance
0
100
200
300
400
500
Central California Foothills and Coastal Mountains
Central California Valley
Coast Range
Southern California Mountains


Relative abundance
0
100
300
500
700
2000
3000
4000
5000
6000
7000
8000
Median NDVI


Relative abundance
0
100
300
500
0
200
400
600
800
Precipitation (mm)


Relative abundance
0
100
300
500
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Proportion Grass

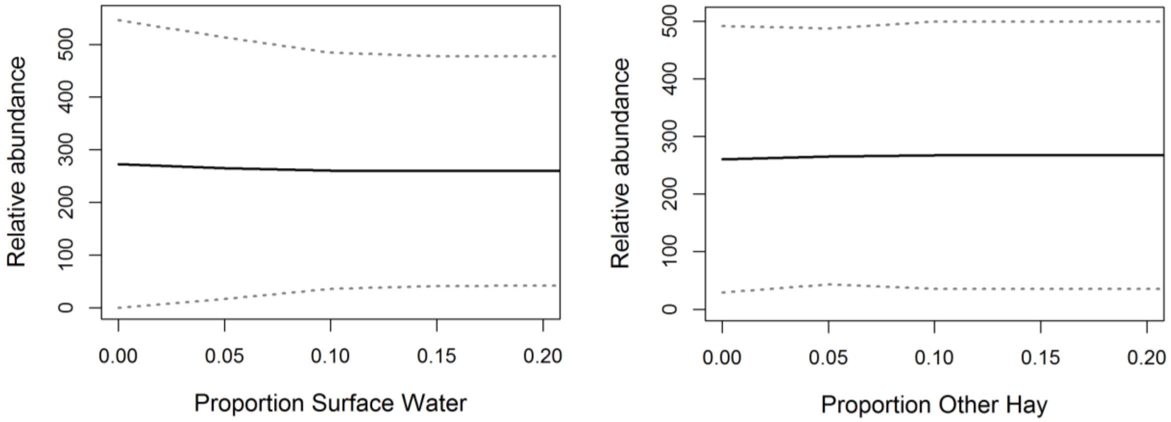


Figure 6. Response plots for the relationship between predicted TRBL relative abundance and environmental covariates explaining ≥1% of the model deviance in the model.

Consistent with the “hurdle model” approach, we predicted TRBL abundance only in areas identified as suitable by the presence-absence model. Predicted TRBL abundance across California in April 2014, based on the environmental covariate relationships determined in the abundance model, is shown in Figure 4.

3.5 DISCUSSION

Models of presence-absence and abundance provide insights into the most important landscape conditions surrounding TRBL nesting colonies. Variable response plots identify potential thresholds in landscape composition above which colony occurrence increases. These occur at approximately 30% and 80% grassland cover (2360 and 6280 ha) and 15% alfalfa (1180 ha) within a 5km-radius circle, and 5% surface water (4 ha) within a 500m-radius circle. Relative abundance increases above approximately 15% alfalfa cover (1180 ha) and more than two dairies within 500m-radius circle. These thresholds and associated minimum areas can be used to inform restoration efforts by setting habitat area targets.

Models of presence-absence and abundance performed moderately well overall (32% and 16% of deviance explained, respectively), showing that not all the variation in the location and size of TRBL colonies is explained by the environmental covariates included. The most relevant environmental factor excluded from the models is the presence of suitable nesting substrate. TRBL nests in a variety of substrates, including native stinging nettle and thistle, exotic blackberry, cultivated fields of triticale grain and wetlands (Graves et al. 2013, Holyoak et al. 2014). Region-wide spatial coverages are lacking for some of these layers, which is why the models focus on suitable foraging habitat availability. However, annual fluctuations in the presence of nesting substrate is a key factor in nest site selection. Most recently, rains in early 2016 led to large patches of milk thistle appearing in the Central California Foothills that served as nesting substrate in the breeding season (personal commentary, Bob Mease). The fact that nesting substrate is ephemeral creates challenges for modeling and management.

There were 382 colony locations occupied during the triennial survey in 2008, 2011, or 2014. The paucity of these sites also limits model performance; particularly in the abundance model which is built solely from these data points. The inclusion of eBird checklist data to augment the number of absence observations improved the performance of the presence-absence model notably. Both models would benefit from incorporation of additional data, perhaps from the second breeding season, if those could be standardized to the protocol of the triennial counts.

Outputs reflect areas of potential foraging habitat in April, but other landscape characteristics may be important for TRBL later in the breeding season. The first nesting attempt of the year occur mostly in April across the TRBL range, but colonies often move north for a second nesting attempt in June. It is possible that landscape factors that were not important in April become important later in the season, such as rice plantations (Holyoak et al. 2014) in the Sacramento Valley.

The results presented here provide a useful index of colony site potential, both occurrence and population size, that can be combined with site-specific information on nesting substrate availability. Furthermore, predictions of probability of occurrence and relative abundance can be updated with more recent land cover data to capture annual changes in land cover and vegetation condition. A long-term goal could include updates to these models and data products with each subsequent triennial survey.

4 DROUGHT-RELATED LAND-USE CHANGE

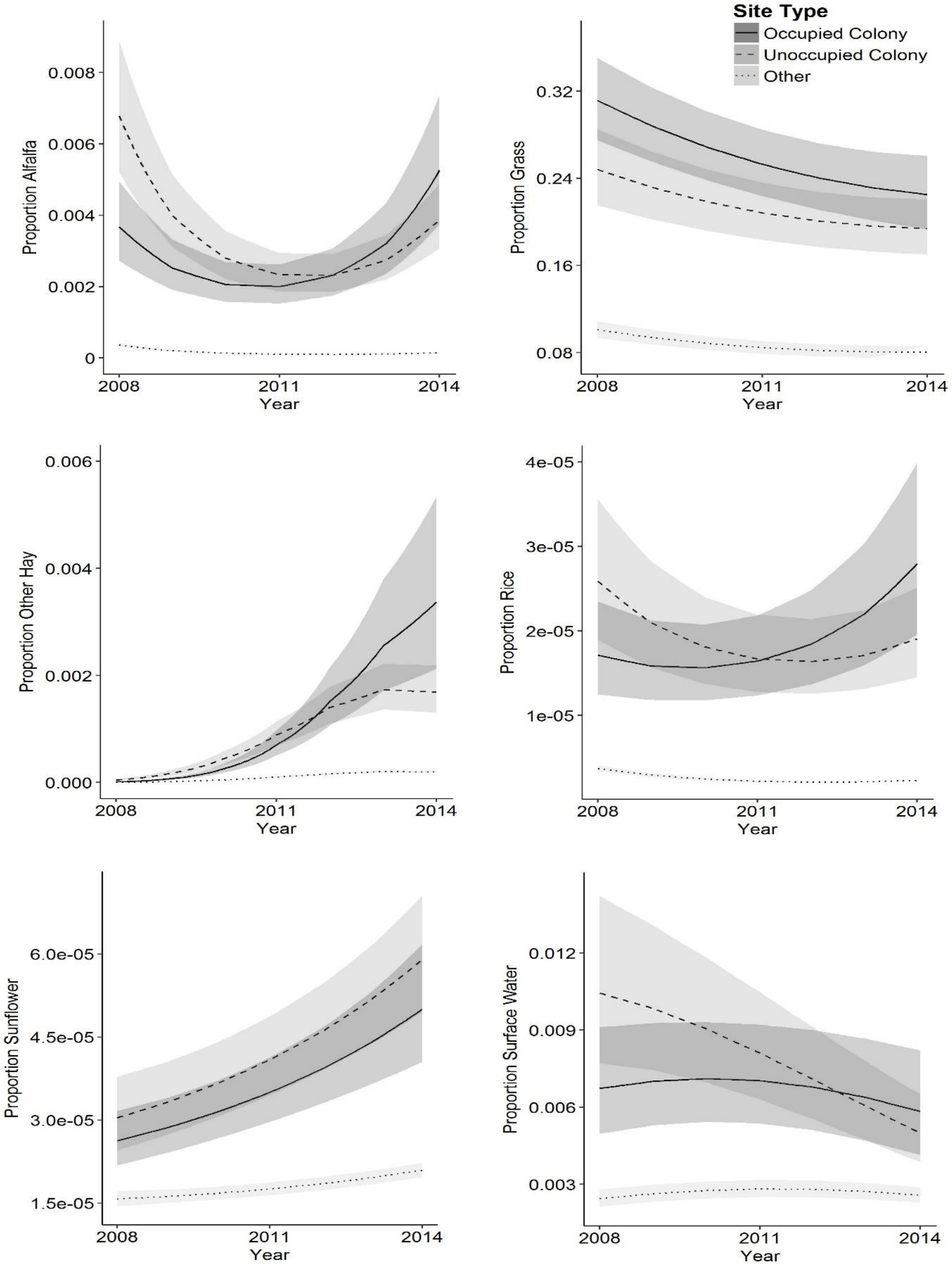
Here, our goal was to look for a signal that recent (2008-2014) land-use changes have reduced the extent of foraging habitat or directly impacted TRBL relative abundance. Drought is generally recognized as a driver of land-use change in California (Soulard and Wilson 2015). We first quantified landscape change focusing on foraging habitat and second considered whether declining forage explains declines in breeding abundance. In addition to foraging habitat, we considered changes in surface water and precipitation.

4.1 ANALYSIS OF LAND-USE CHANGE

Trends in land cover change were analyzed using general linear mixed models in R package *nlme* (Pinheiro et al. 2016). We compiled land cover information from locations surveyed as part of the TRBL Triennial Surveys and entered into eBird (used for TRBL absence locations only) across the four ecoregions included in the foraging habitat selection models. We analyzed land cover change as a function of three site types: occupied TRBL colonies, unoccupied TRBL colonies, and other (i.e., data from eBird, representing locations where TRBL were not observed and colonies are not known to occur). Proportion cover data were logit-transformed and the number of dairies, NDVI, and precipitation data were log-transformed to meet assumptions of normal (Gaussian) linear models. Site type and year (including a quadratic term to model curvilinear relationships) and their interaction were included as fixed effects and location was included as a random effect in the fully parameterized model. AIC-based model selection was used to select fixed effects for inclusion in the final model. Temporal autocorrelation was accounted for using a first-order conditional autoregressive (CAR1) structure as needed (i.e., if the addition of a CAR term improved model fit as measured by AIC). Similarly, heterogeneity in variances between TRBL presence and absence sites was accounted for using weights when this term improved model fit. Fixed effects of land cover change over time were evaluated using R package *effects* (Fox 2003), and plotted using *ggplot2* (Wickham 2009).

4.2 RESULTS

Proportion alfalfa declined then rebounded during 2008-2014 (Fig. 7), and was greater at TRBL colonies than other sites ($P < 0.001$). However, the proportion of alfalfa did not differ between occupied and unoccupied TRBL colonies ($P = 0.86$), suggesting that change in alfalfa cover over time does not explain declines in TRBL occurrence or abundance. Grass cover significantly declined over time at all sites ($P < 0.001$). However, grass cover did not differ between occupied and unoccupied colonies ($P = 0.29$) or between colonies and other sites ($P = 0.36$). Proportion other hay increased over time at all sites ($P < 0.001$), and occupied colonies had significantly more other hay on the landscape than other sites ($P =0.002$) but not unoccupied colonies ($P = 0.15$). Unoccupied TRBL colonies had significantly higher proportion rice than other sites ($P = 0.005$), but rice cover did not change over time ($P = 0.13$). Proportion sunflower did not change over time ($P = 0.08$) and did not differ between occupied and unoccupied colonies ($P = 0.99$), though it was significantly lower in other sites ($P < 0.01$).


Site Type
Occupied Colony
Unoccupied Colony
Other
Proportion Alfalfa
0.008
0.006
0.004
0.002
0
Proportion Grass
0.32
0.24
0.16
0.08
Proportion Other Hay
0.006
0.004
0.002
0.000
Proportion Rice
4e-05
3e-05
2e-05
1e-05
Proportion Sunflower
6.0e-05
4.5e-05
3.0e-05
1.5e-05
Proportion Surface Water
0.012
0.009
0.006
0.003
2008
2011
2014
Year

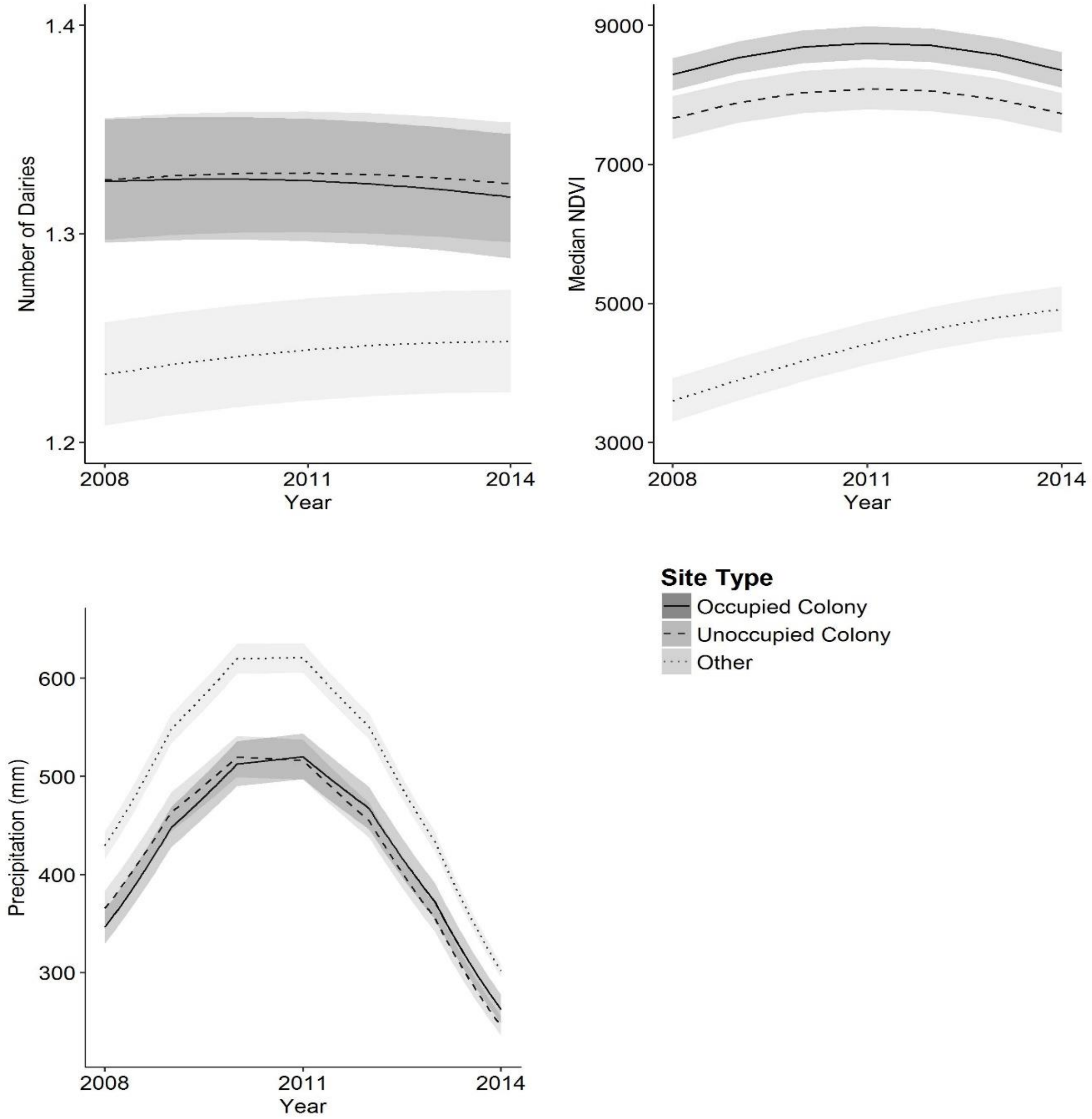


Figure 7. Trends in land cover during 2008-2014 in occupied TRBL colonies, unoccupied TRBL colonies and other sites (from eBird).

Surface water cover significantly declined over time at all sites, but at a significantly faster rate in unoccupied colonies than either occupied colonies ($P = 0.02$) or other sites ($P < 0.001$). On average both occupied ($P = 0.02$) and unoccupied colonies ($P < 0.001$) had more surface water cover than other sites. The number of dairies slightly declined in both occupied and unoccupied TRBL colonies but not at other sites, where there were also fewer dairies on average ($P < 0.001$). NDVI was significantly higher in occupied and unoccupied colonies than other sites ($P < 0.001$), but increased over time only at non-colony sites ($P < 0.001$). Precipitation peaked then declined at all sites, but was highest at non-colony sites on average ($P < 0.04$).

4.3 DISCUSSION

Our analyses showed that trends in land cover are highly variable in California. California experienced a long-term drought that was alleviated somewhat by heavy rains in 2011. Drought conditions were apparent in the trends of four land cover metrics which exhibited similar curvilinear responses. Surface water and NDVI both increased with precipitation, while alfalfa and rice exhibited opposite responses with the lowest cover estimates in 2011. This suggests that drought conditions had both positive and negative effects on TRBL, as occurrence and abundance increased with the amount of both alfalfa (more in the drier years) and surface water (more in the wettest year) on the landscape.

Two declining trends in land cover appeared to be particularly informative in explaining TRBL population declines. First, grass cover, the second most important predictor of TRBL occurrence (Fig. 3), significantly declined over time. Second, surface water significantly declined over time in unoccupied colonies but not in occupied colonies, suggesting that permanent surface water is a critical feature of persistent TRBL colonies.

Finally, mean cover of nearly all land cover types, as well as the number of dairies and median NDVI, were significantly higher in both occupied and unoccupied colonies than sites where TRBL were not known to occur. This highlights the importance of conserving both current and historic TRBL colony sites, as they provide key habitat characteristics that are of limited availability elsewhere in the state.

5 CONSERVATION AND RESTORATION PRIORITIES

We use results from the presence-absence and abundance models described above (Section 3: Landscape Measures of Foraging Habitat) to map core and potential TRBL breeding habitat in regions well-sampled by the triennial surveys. Core habitats have been defined broadly as areas meeting minimum requirements for habitat composition and configuration. For example, Johnson et al. (2010) and Wilsey et al. (2016) identified grassland priority conservation areas in the Prairie Pothole and Midwest Regions based on patch size and the proportion of surrounding habitat. Here, we define core areas based on outputs from our combined presence-absence and abundance models projected to 2014 land cover.

5.1 MAPPING CONSERVATION AND RESTORATION PRIORITIES

We combined outputs from the occurrence and relative abundance models to map core TRBL habitat in a region encompassing the Central Valley, Southern California Mountains, and Central California Foothills and Coast Range level III ecoregions (EPA 2013). In the "hurdle model" approach, core areas must meet all criteria for habitat suitability identified in our presence-absence and abundance models. The presence-absence threshold (0.02) was selected to allow omission of only 5% of occupied colony sites in the triennial survey dataset: a conservative threshold that places high value on known colonies. We then examined maps of core habitat based on the mean, median, and third quantile of relative abundance across the predicted area of occurrence to identify an appropriate relative abundance threshold. Identifying as core habitat only those grid cells with predicted relative abundance above the median predicted value (122 individuals) resulted in only the smallest colonies being left out of the final core habitat map, whereas setting the threshold lower (mean relative abundance) was too inclusive and higher (third quantile) was to restrictive.

The “hurdle model” approach used species-habitat relationship from both the presence-absence and relative abundance models to define core habitat criteria. Examining the variable response plots for each model (Fig. 3 & 6, above) revealed minimum habitat requirements. Roughly, for a grid cell to be considered core, early season foraging habitat alfalfa or grassland coverage must have been greater than 15% (1180 ha) or 30% (2360 ha), respectively, within 5 km of a grid cell and there must have been >5% surface water (4 ha) within 500 m of a grid cell. Furthermore, the largest colonies had higher proportions of alfalfa and were within 5 km of at least two dairies. Greener vegetation (i.e. median NDVI) also occurred near sites of greater abundance. Core areas were mapped and area quantified by ecoregion and land ownership class.

By examining the species-habitat relationships defined in the presence-absence and relative abundance models, we identified three influential habitat criteria that could be improved through restoration/ management (hereafter restoration): the proportion of alfalfa and grassland within 5 km, and the proportion of surface water within 500 m. We explored increasing each of these measures and the corresponding impact on modeled relative abundance to identify areas with high restoration potential. For each restoration action, we generated modeled occurrence and abundance maps under a scenario which doubled the current area at each grid cell. We then overlaid this with the core area map for 2014 and areas mapped as core habitat under the restoration scenario that were not already identified as core habitat in 2014 were considered potential habitat. This was done iteratively for alfalfa, grassland, and surface water.

5.2 RESULTS

Modeled TRBL core foraging habitat in 2014 amounted to more than 6 million acres (Table 1). The majority of this (63%) occurred in the Central Valley followed by the Central Foothills and Coastal Mountains (35%). Only 6.9% of this core habitat was protected according the California Protected Areas Database (GreenInfo Network 2013). Protected habitats were divided among federal agencies, local government, and non-profit organizations (Table 2).

Table 1. Acres of modeled TRBL core foraging habitat in 2014 by ecoregion.

Ecoregion Name	Acres
Central California Foothills and Coastal Mountains	2,383,240
Central California Valley	4,321,270
Coast Range	161,253
Southern California Mountains	1,261

Table 2. Core habitat area by land owner, excluding private lands. List includes only landowners whose holdings are at least 0.1% of the total core habitat. Only 5.6% of the core habitat falls within the agencies listed here.

Managing Agency	Acres within Core Habitat	% of Core Habitat
California Department of Fish and Wildlife	89,154	1.3%
U.S. Fish and Wildlife Service	58,439	0.9%
East Bay Regional Park District	36,683	0.5%

Managing Agency	Acres within Core Habitat	% of Core Habitat
California Department of Parks and Recreation	32,313	0.5%
East Bay Municipal Utility District	23,476	0.3%
California Department of Water Resources	20,090	0.3%
U.S. National Park Service	19,576	0.3%
U.S. Bureau of Land Management	17,991	0.3%
The Nature Conservancy	14,813	0.2%
Contra Costa Water District	10,135	0.1%
County of Santa Clara Parks and Recreation Department	9,989	0.1%
Solano Land Trust	9,855	0.1%
City and County of San Francisco Public Utilities Commission	9,405	0.1%
U.S. Bureau of Reclamation	7,958	0.1%

A simulated doubling in the coverage of alfalfa, grass, and surface water resulted in 0.6-61.2% increases in core habitat area (Table 3). The majority of potential core habitat resulted from simulated increases in alfalfa, followed by grass. Potential core foraging habitat from alfalfa expansion was primarily found in the Central Valley ecoregion, whereas grassland expansion created potential habitat in the Sierra Foothills and Coastal Mountains (Fig. 8). Increasing surface water created relatively less potential habitat and most of that was concentrated in the Central Valley.

Table 3. Proportion of area gained through simulated restoration scenarios representing a doubling of current coverage.

Type	Acres	Proportion gained
Core	6,867,024	
Surface water	6,906,680	0.6%
Grass	10,432,700	51.9%
Alfalfa	11,071,800	61.2%

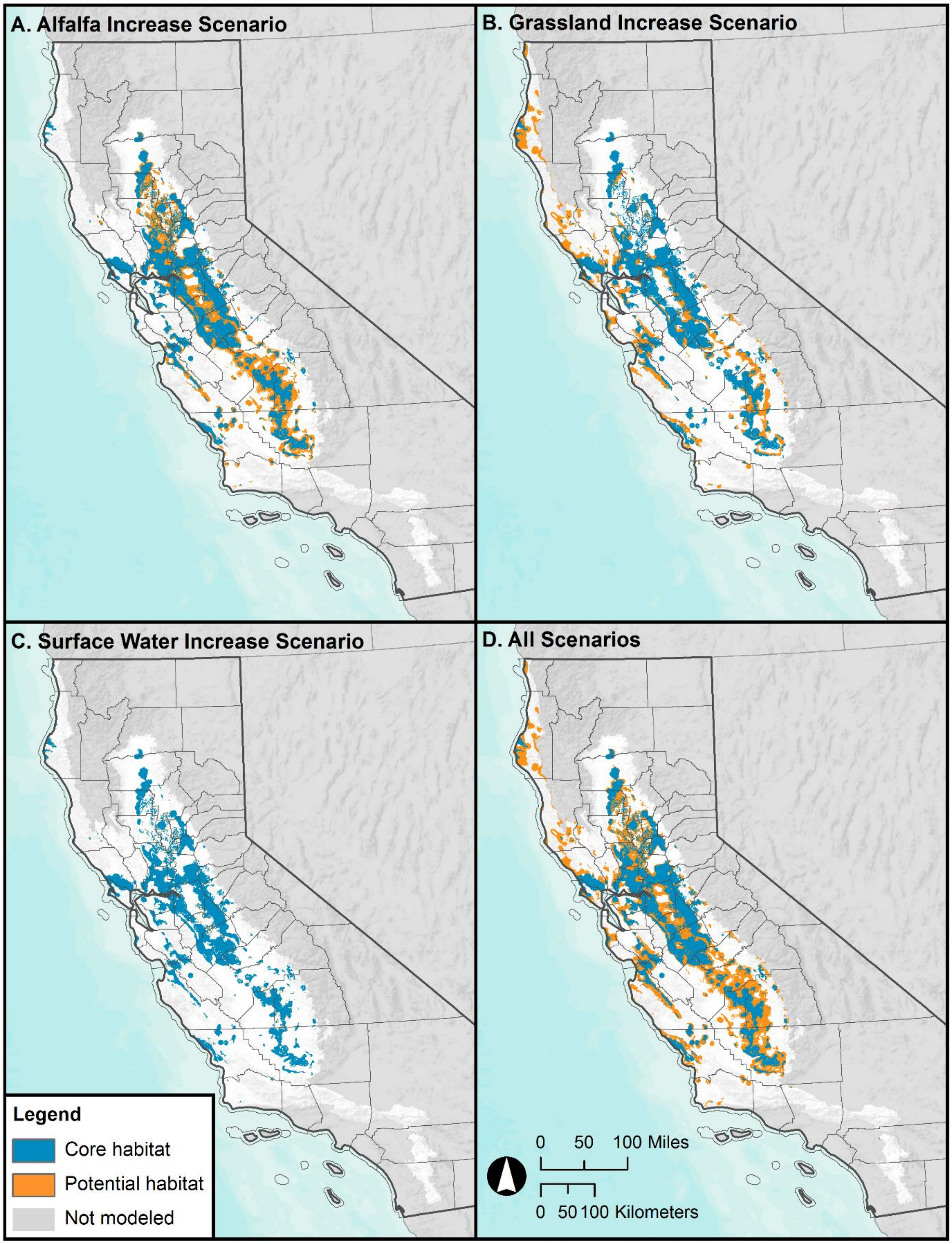


Figure 8. Core and potential Tricolored Blackbird habitat under simulated restoration scenarios for doubling (A) alfalfa, (B) grassland, (C) surface water, and (D) the union of all scenarios.

5.3 DISCUSSION

Results quantified and mapped the potential to increase TRBL core foraging habitat within the study region. The simulations used to identify areas of high habitat potential applied a simple rule: the doubling of existing habitat coverage. We used this approach, as opposed to more sophisticated simulations of land cover change (e.g. Sohl et al. 2014), because of its simplicity and because it automatically defined restoration potential based on the current land cover at a site. For example, under this approach areas lacking alfalfa in 2014 would not be simulated to have sufficient alfalfa under a restoration scenario. Conversely, potential habitat under the alfalfa scenario already have some alfalfa and likely have the appropriate soil and water resources to support expansion of alfalfa cultivation. However, this simple approach risks under-estimating the potential for landscapes to support TRBL. To explore this, we also generated maps of potential habitat by increasing all grid cells to 30% alfalfa or grassland cover and 5% surface water. This did not result in much change in the coverage of potential habitat under the increased grassland and surface water scenarios, but did result in nearly wall-to-wall potential habitat in the alfalfa scenario. We therefore opted for the simpler approach which drew upon present-day landcover to inform where restoration work could occur.

Maps of potential habitat lack one key element of colony site selection: substrate. Therefore, future conservation and restoration efforts much include site visits to verify the presence of appropriate substrate. We proposed a tiered approach towards habitat conservation and restoration (Table 4).

Table 4. Habitat conservation and restoration priorities for early breeding season TRBL foraging habitat.

Tier	Description	Recommendation
1	Core habitat with appropriate nesting substrate (verified locally)	Priority for conservation (e.g. acquisition or easements).
2	Core habitat without nesting substrate	Targeted for planting of substrate or agreements with farmers to delay harvests.
3	Potential habitat with nesting substrate	Targeted for restoration by increasing coverage of alfalfa, grasslands, or water.
4	Potential habitat without nesting substrate	Targeted for restoration by planting non-invasive substrates (e.g. thistle and nettles) in addition to increasing coverage of alfalfa, grasslands, or water.

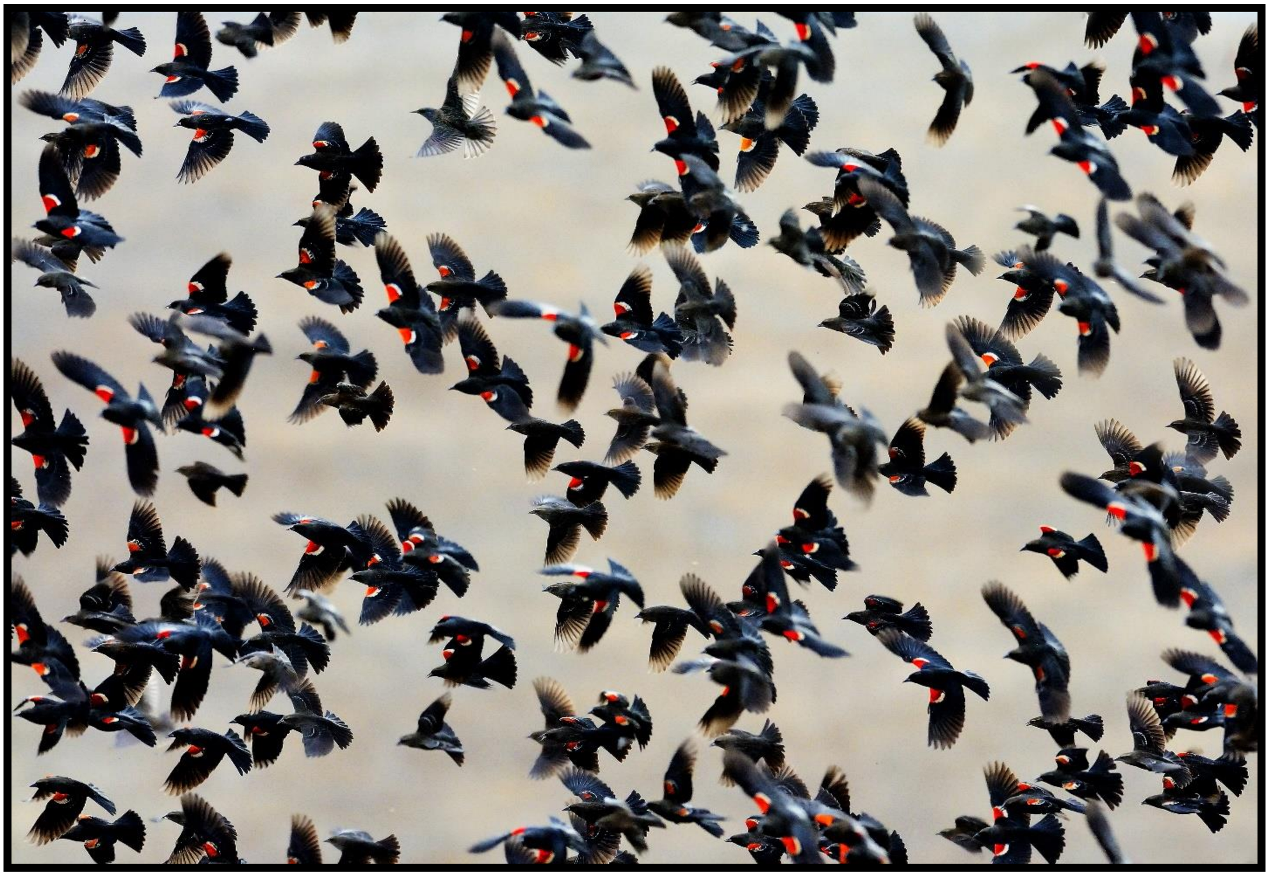


Photo Credit: © Jerry Ting

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