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Acoustic and camera surveys inform models of current and future vertebrate distributions in a changing desert ecosystem

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Abstract

Aim: Maintaining biodiversity in the face of land use and climate change is a paramount challenge, particularly when distributions of many species remain incompletely known. Emerging technologies help address this data deficiency by facilitating the collection of spatially explicit data for multiple species from multiple taxa. In this study, we combine acoustic and visual sensor surveys to inform conservation and land use planning in an area experiencing rapid climate and land use change.

Location: Mojave Desert, California, United States.

Methods: We deployed camera traps and acoustic detectors at 210 sites between March and July 2016. We identified photographic detections of mammals and acoustic recordings of songbirds to the species level and used multispecies occupancy models to estimate and evaluate species' occupancy probabilities. We then extrapolated model results to the region and forecasted how projected climate and land use changes might affect species' occupancy probabilities in 50 years. Lastly, we identified areas with high conservation value (i.e., high relative species richness) now and in 50 years, and related the distributions of these areas to land use designations.

Results: We detected 15 mammal and 68 songbird species. At the community level, occupancy decreased with increasing temperatures and distances to woodlands. We forecasted that occupancy probabilities and areas with high conservation value would decline in 50 years due to projected increases in maximum temperatures and identified that up to 43%, 24% and 27% of land designated for renewable energy development, recreation and military activities, respectively, encompassed these high value areas.

Main conclusions: Cooler areas close to woodlands and water are of high conservation value to mammals and songbirds in the Mojave. These areas will become increasingly limited with changing climate, however, making their protection from human disturbance imperative. We encourage continued use of visual and acoustic sensors across large spatial, temporal and taxonomic scales as tools to inform land use and wildlife conservation.

KEYWORDS
acoustic recorder, camera trap, climate change, land use planning, Mojave Desert, multispecies occupancy model, species richness

1 | INTRODUCTION

Maintaining the world's tremendous diversity of life is a paramount and daunting challenge amid the land use and extractive activities of 7.4 billion people and a rapidly changing climate (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Jetz, Wilcove, & Dobson, 2007; Walther et al., 2002). Human actions, including the conversion, degradation and fragmentation of natural habitats, and the direct persecution of wild vertebrates (e.g., retaliatory killings, subsistence hunting, or poaching) are placing unprecedented pressures on biodiversity globally (Jetz et al., 2007; Newbold et al., 2015). Concurrently, human-induced climate change is increasing the quantity and severity of environmental stressors such as drought, fire, or disease and insect outbreaks, and driving shifts in species' geographic ranges and community structures (Bentz et al., 2010; Dale et al., 2001; IPCC, 2007; Seager et al., 2007; Walther et al., 2002). By many forecasts, without active management efforts, the effects of future land use and climate change on biodiversity will be immense (Barnosky et al., 2011).

Fine-grain, species-specific data collected across large spatial and temporal scales is vital to quantifying the pace of biodiversity change, to identifying large-scale ecological stressors and to designing land use and conservation plans that effectively minimize negative impacts on vertebrate populations, (Bellard et al., 2012; Cameron, Cohen, & Morrison, 2012; Jetz, McPherson, & Guralnick, 2012; Pereira et al., 2013; Theobald et al., 2015). Further, without biodiversity data it is challenging for wildlife managers and land use planners to make proactive versus reactive decisions. Proactive decisions are those that if implemented, and if projected ecosystem changes are accurate, will benefit biodiversity in the future (e.g., conserving areas projected to be important movement corridors or climate refugia), whereas reactive decisions involve responding to impacts as or after they occur (Palmer et al., 2008). Despite the clear importance of empirical data for biodiversity conservation, the infrastructure required to collect and analyse comprehensive monitoring data is often lacking (Ahumada, Hurtado, & Lizcano, 2013; Schmeller et al., 2015).

New, emerging technologies are helping to address these data deficiencies by facilitating the collection of spatially explicit, landscape-level data for multiple species from multiple taxa. Arrays of fixed acoustic sensors, for example, can record bird, bat, anuran and insect taxa that emit species-specific sounds (Aide et al., 2013; Blumstein et al., 2011). Visual sensors (i.e., camera traps), alternatively, use motion and heat-sensing infrared technology to provide photographic detections for a diversity of mammal, bird and fish species (Rich et al., 2017; Steenweg et al., 2017). Both sensor types have greatly improved inferences on the population dynamics of rare or elusive species, and have enabled the quantification and evaluation of species distributions, community richness, temporal activity patterns, population trends and inter- and intraspecific interactions (Aide et al., 2013; Blumstein et al., 2011; Rich et al., 2017; Steenweg et al., 2017).

In this study, we explore the utility of combining acoustic and visual sensor surveys to inform land use planning and biodiversity management in a region experiencing rapid change, the Mojave Desert of California. The Mojave Desert is a 32.1 million acre area that falls within the North American desert complex, one of the five most biologically diverse wilderness areas in the world (Mittermeier et al., 2002). In addition to harbouring rich biodiversity, the Mojave Desert provides critical habitat for many threatened and endangered species (Flather, Knowles, & Kendall, 1998; Randall et al., 2010). Similar to many other regions around the world, climate change and a multitude of human-mediated land use pressures are threatening the Mojave Desert's diverse fauna (Gibson, Wilman, & Laurance, 2017; LaDochy, Medina, & Patzert, 2007; Leu, Hanser, & Knick, 2008; Lovich & Bainbridge, 1999; Seager et al., 2007). Mean annual temperatures have increased by over 2°C in the last 50 years while precipitation has decreased, causing the region to become increasingly hot and arid (LaDochy et al., 2007; Rapacciuolo et al., 2014; Seager et al., 2007). Land use changes triggered by urbanization, military activities and recreation (e.g., off-road vehicle use), alternatively, have resulted in widespread habitat loss, fragmentation and degradation in this region (Leu et al., 2008; Lovich & Bainbridge, 1999). Further, the Mojave Desert is experiencing development pressures from the renewable energy sector as California increasingly invests in wind and solar energy production (Cameron et al., 2012; Gibson et al., 2017; Hernandez, Hoffacker, Murphy-Mariscal, Wu, & Allen, 2015). An understanding of species distributions and habitat requirements is needed to minimize the potentially adverse impacts of climate and land use pressures on biodiversity in this region.

We focused our survey approach in the Mojave Desert on songbird and mammal communities. The specific objectives of our study were threefold. Our first objective was to use data from acoustic and visual sensor surveys to model current occupancy probabilities for terrestrial mammal species weighing >0.5 kg and songbird species in the Mojave Desert. We expected that the spatial distributions of vertebrates would be most strongly influenced by topography, water availability, woodland habitat, urban development and climate (Epps, McCullough, Wehausen, Bleich, & Rechel, 2004; Jetz et al., 2007; Ordeñana et al., 2010; Walther et al., 2002). Our second objective was to use occupancy model outputs to identify areas with high conservation value for mammal and songbird communities, and to relate the distributions of these areas to five major land designations (i.e., areas designated for federal protection, conservation planning, recreation, military and energy development). Our final objective was to demonstrate how modelled occupancies and projected climate and land use changes can be integrated to predict species' occupancy probabilities and the availability/distribution of areas with high conservation value in 50 years. Ideally, through these steps, we can provide a better understanding of mammal and songbird populations in the Mojave Desert that can inform proactive land use and biodiversity management strategies and the prioritization of conservation actions. Furthermore, as this is among the first studies to integrate acoustic and visual sensor data, we hope this work provides a timely example of how emerging technologies can facilitate multispecies and multi-taxa data collection.

2 | METHODS

2.1 | Study area and design

The Mojave Desert ecoregion of California, as defined by the U.S. Department of Agriculture (USDA, 2016), is a 66,830 km^2 area with elevations ranging from −83 to 2,414 m ($\bar{x}$ = 796 m). The study area encompasses over 140 different vegetation communities with the predominant National Vegetation Classification (NVC) macrogroup being Mojave-Sonoran semi-desert scrub (e.g., *Larrea tridentata* and *Ambrosia dumosa*; Menke, Reyes, Glass, Johnson, & Reyes, 2013; USNVC, 2016). Other vegetation macrogroups included, for example, Great Basin-intermountain dry shrub/grassland (e.g., *Yucca brevifolia*), desert alkali-saline marsh, playa, and shrubland (e.g., *Atriplex spinifera*), warm desert xeric-riparian scrub (e.g., *Senegalia greggii*), and warm semi-desert cliff, scree, and rock vegetation (e.g., *Atriplex hymenelytra*). The eastern border of our study area was the California state line, but we note that the Mojave Desert extends into Nevada, Arizona and the southwest corner of Utah.

We surveyed 210 sites across the California portion of the Mojave Desert region between March and July 2016 (Figure 1). We identified survey locations by first selecting a spatially balanced random sample of hexagons, stratified by vegetative community, from the USDA Forest Inventory and Analysis program's hexagon grid (hexagon radius is ~2.6 km). We then randomly selected 1–3 survey locations within each hexagon, which were spaced by 1–2 km and stratified by vegetative community. Survey sites covered a broad range of elevations, ranging from −75 m in Death Valley National Park to 1,630 m in the Mojave National Preserve (Appendix S1).

2.2 | Camera trap and acoustic recorder surveys

At each survey location, we deployed a PC900 camera trap (Reconyx) and a SM3-BAT bioacoustic recorder with microphone (Wildlife Acoustics, Inc., hereafter termed ARU). We cable-locked cameras and ARUs to securely placed T-posts 1-m and 2-m above the ground, respectively; T-posts were separated by at least 30 m. If T-post mounting was not possible, we secured devices to a tree or other rigid vegetation.

Cameras were deployed for an average of 34 days (*SD* = 7.6) and baited during their initial deployment in an attempt to maximize detection probabilities (Karanth, Nichols, 2011). Our goal was to increase the probability of photographing mammals within the vicinity of the camera rather than attracting mammals from long distances. Thus, we used baits that were detectable at short distances including a 250 g salt lick, 100 ml of rolled oat–peanut butter mixture and 150 g of fishy cat food. We programmed cameras to take three photographs at each trigger event, with a delay of one second between trigger events. After the field season, we identified photographic detections to the species level, omitting photographs when this was not possible (e.g., blurry images).

We programmed ARUs to record three, 5-min sessions on three consecutive days during the survey period. The first session was at 30 min before sunrise, the second at sunrise and the third at 30 min after sunrise (Furnas & Callas, 2015). We had an expert in aural identification of California desert birds review each 5-min recording and identify bird species by song or call. To aid in bird identification, the expert examined spectrograms in Raven Pro software (v. 1.5; Cornell Lab of Ornithology Bioacoustics Research Program). We omitted recordings that could not be identified to the species level and, in an

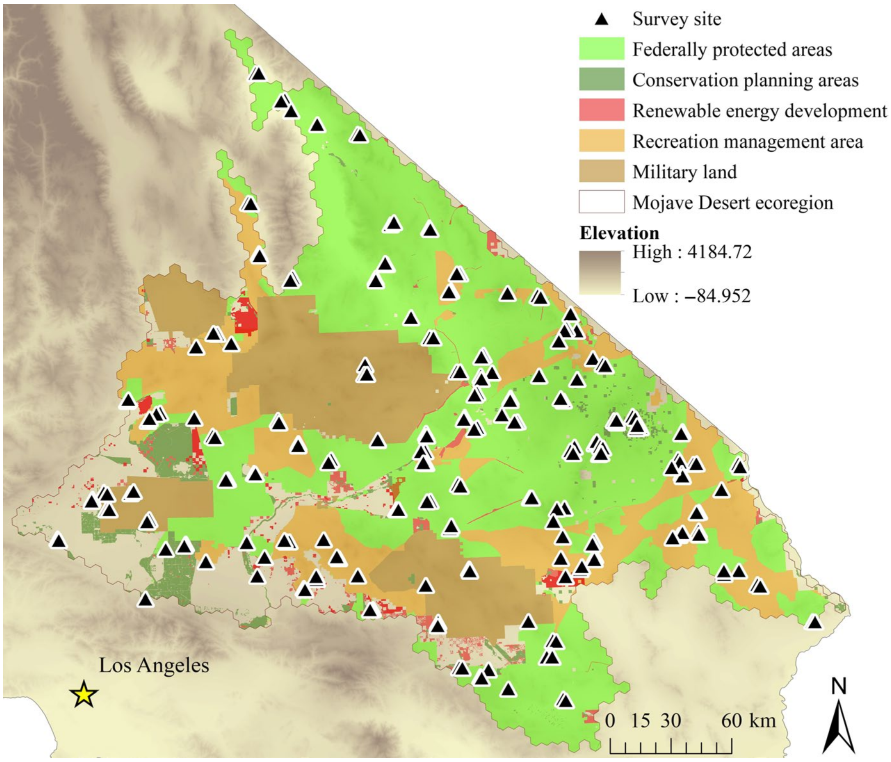

FIGURE 1 Survey site locations in the Mojave Desert of California, 2016, and land designations across the region

effort to ensure species were similar ecologically, we restricted our analysis to songbirds (i.e., species in the order Passeriformes; Barker, Cibois, Schikler, Feinstein, & Cracraft, 2004). The specialist also classified the level of background noise (e.g., wind, rain, vehicle and air traffic) during each recording using an ordinal variable ranging from zero, indicating no noise, to four, indicating loud noise.

2.3 | Spatial covariates of occupancy and detection

We expected that slope, water availability, habitat heterogeneity, urban development and climate would influence wildlife distributions across the Mojave Desert. We used the 30-m resolution National Elevation Dataset (USGS, 2016) to calculate and extract slope values for each sampling site location in ArcMAP 10.4.1 (ESRI). We used Global Surface Water Explorer (Pekel, Cottam, Gorelick, & Belward, 2016) to identify permanent and seasonal water sources, United States Geological Survey (USGS) land use data (Sleeter, Wilson, Sharygin, & Sherba, 2017) to identify urban development and California Department of Fish and Wildlife (CDFW) vegetation data (CDFW, 2017) to identify the NVC macrogroup “intermountain pinyon-juniper woodlands.” We then measured the distances from each site to the nearest water source, developed area and pinyon-juniper woodland in ArcMap. We chose to estimate the distances to these environmental features, as compared to their coverage within a certain area surrounding the site (e.g., a 1- or 5-km^2 buffer), because we were examining a broad range of species with varying area requirements and our multispecies models required covariate values to be consistent across all species. We included pinyon-juniper woodlands, specifically, because they provide an important form of vertical habitat heterogeneity in the Mojave Desert, but we note that other vegetation types and communities (e.g., Joshua trees—*Y. brevifolia*) were also likely important. Lastly, to represent climate, we used 30-year (1981–2010), 270-m resolution summary data from the 2014 California Basin Characterization Model (BCM; California Landscape Conservation Cooperative, 2014). We used this dataset to ensure the temporal and spatial resolution of our current climate values would be consistent with that of our projected climate values. We extracted site-specific values for mean annual precipitation (cm), maximum monthly temperature (°C) and climatic water deficit, which was a function of potential and actual evapotranspiration (Flint, Flint, Thorne, & Boynton, 2013).

The phenology of birds' vocal behaviours can change over the course of a breeding season (Furnas & McGrann, 2018) and mammals' movement and activity patterns may fluctuate based on environmental factors and human activity (Ordiz, Sæbø, Kindberg, Swenson, & Støen, 2017). Thus, we expected that a species' probability of being detected may vary based on human impact, time of year and temperature. To quantify human impact at each sampling site, we extracted values from the USGS human footprint model (USGS, 2016b), and to represent time of year, we included mean Julian day and its quadratic term. To represent temperature, we used 4-km resolution daily temperature data from PRISM (Prism Climate Group 2018). Daily temperature and Julian day were highly correlated (r = 0.77). Thus we only retained Julian day for our analyses because Julian day had a stronger univariate effect size, and we did not want to confound differences in phenology with differences in occupancy (Strebel, Kéry, Schaub, & Schmid, 2014). Lastly, for songbirds, we also included mean background noise, which can impede the audibility and identification of bird species.

2.4 | Multispecies occupancy models

We used multispecies hierarchical occupancy models to estimate the probability species i occurred within the area sampled by a camera trap or ARU during our survey period (i.e., occurrence; Dorazio & Royle, 2005; Iknayan, Tingley, Furnas, & Beissinger, 2014). Multispecies models link species-specific detection and occupancy using community-level hyper-parameters which specify the mean response and variation among species within the community to a respective covariate (Kéry & Royle, 2008; Zipkin, Royle, Dawson, & Bates, 2010). Linking occurrence models for individual species within a hierarchical model results in a more efficient use of data, increases precision in estimates of occupancy and allows for assessments of ecological variables at both the species level and community level (Kéry & Royle, 2008; Iknayan et al., 2014; Zipkin DeWan, & Andrew Royle, 2009). Further, the models produce estimates of species richness (i.e., number of species in the community and at each sampling location).

Occupancy models distinguish the true absence of a species from the non-detection of a species (i.e., species present but not photographed/recorded) using spatially or temporally replicated survey data. For each sampling location, we treated each 24-hr camera trapping period ($\bar{n}$ = 34) and each 5-min acoustic recording (n = 9) as a repeat survey at that particular site. For our camera trap model and for our ARU model, we specified the occurrence probability (ψ) for species i at site j as:

$$\begin{gathered}\text{logit}\left(\psi_{ij}\right) = \alpha 0_i + \alpha 1_i\,(\text{slope})_j + \alpha 2_i\,(\text{distance to water})_j \\ + \alpha 3_i\,(\text{distance to pinyon juniper})_j + \alpha 4_i\,(\text{maximum temperature})_j \\ + \alpha 5_i\,(\text{distance to developed area})_j\end{gathered}$$

We did not include annual precipitation and climatic water deficit in our final model because they were highly correlated with maximum monthly temperature (r > |0.8|)—the climatic variable that had the strongest influence on mammal and songbird occupancy in preliminary analyses. We also included human impact and Julian day and its quadratic term as covariates for detection in both models, with the addition of background noise in the ARU model. We linked species-specific models using a mixed modelling approach where we assumed species-specific parameters were random effects derived from a normally distributed, community-level hyper-parameter (Zipkin et al., 2010). Given we evaluated two occupancy models (i.e., one model for the camera trap data and one for the ARU data), we had separate community-level parameters for mammals and for songbirds. We estimated posterior distributions of parameters using Markov Chain Monte Carlo implemented in JAGS (Plummer, 2011) through program *R*. We generated three chains of 50,000 iterations

TABLE 1 Mammal species photographed (a) and songbird species recorded (b) during camera trap and automated recorder surveys in the Mojave Desert of California in 2016, numbers of detections (*n*), projected estimates of occupancy across the region (ψ) and site-level detection probabilities (p^*)

(a)

Common name	n	ψ	p^*	Common name	n	ψ	p^*
Coyote	204	0.37	0.93	Bighorn sheep	68	0.03	1.00
Opossum	2	0.01	0.89	Raccoon	3	0.01	0.95
Black-tailed jackrabbit	1,090	0.70	1.00	Spotted skunk	7	0.04	0.40
Bobcat	107	0.20	0.83	Audubon's cottontail	485	0.22	1.00
Striped skunk	4	0.01	0.96	American badger	44	0.19	0.68
Mule deer	92	0.07	0.93	Grey fox	48	0.05	0.91
CA ground squirrel	1	0.01	0.64	Kit fox	370	0.41	0.98
Rock squirrel	10	0.01	0.94				

(b)

Common name	n	ψ	p^*	Common name	n	ψ	p^*	Common name	n	ψ	p^*
Ash-throated flycatcher	272	0.31	0.99	Cliff swallow	3	0.07	0.34	Ruby-crowned kinglet	3	0.09	0.19
Barn swallow	1	0.04	0.30	Common raven	168	0.47	0.74	Rufous-crowned sparrow	7	0.02	0.70
Black-chinned sparrow	4	0.02	0.71	Common yellowthroat	25	0.02	1.00	Rock wren	147	0.19	0.93
Bell's sparrow	179	0.20	0.93	Crissal thrasher	53	0.12	0.67	Red-winged blackbird	31	0.02	1.00
Bendire's thrasher	5	0.13	0.22	Dark-eyed junco	1	0.03	0.41	Say's phoebe	63	0.13	0.90
Bell's vireo	5	0.01	0.94	Fox sparrow	3	0.05	0.33	Scott's oriole	41	0.11	0.81
Bewick's wren	80	0.10	0.97	Golden-crowned sparrow	1	0.03	0.41	Song sparrow	12	0.02	0.84
Blue-grey gnatcatcher	25	0.06	0.81	Great-tailed grackle	2	0.06	0.28	Spotted towhee	4	0.03	0.52
Brown-headed cowbird	8	0.05	0.49	Hermit thrush	1	0.03	0.36	Verdin	72	0.11	0.96
Black-headed grosbeak	2	0.06	0.33	House finch	149	0.26	0.95	Vesper sparrow	3	0.01	0.66
Blue grosbeak	10	0.01	1.00	Horned lark	352	0.42	0.95	White-crowned sparrow	113	0.50	0.18
Black phoebe	1	0.03	0.42	House wren	1	0.03	0.50	Western kingbird	6	0.02	0.63
Brewer's blackbird	7	0.11	0.27	Juniper titmouse	1	0.03	0.41	Western meadowlark	1	0.03	0.39
Brewer's sparrow	27	0.11	0.23	LeConte's thrasher	68	0.19	0.81	Western scrub-jay	24	0.04	0.97
Black-tailed gnatcatcher	85	0.19	0.90	Loggerhead shrike	81	0.34	0.69	Western tanager	1	0.03	0.42
Black-throated sparrow	636	0.56	1.00	Marsh wren	16	0.02	1.00	Western wood-pewee	1	0.03	0.40
Bullock's oriole	8	0.05	0.52	Northern mockingbird	64	0.10	0.94	Wilson's warbler	5	0.06	0.39
Bushtit	13	0.04	0.81	Northern rough-winged swallow	3	0.03	0.46	White-throated swift	7	0.06	0.48

(Continues)

TABLE 1 (Continued)

(b)

Common name	*n*	*ψ*	*p**	Common name	*n*	*ψ*	*p**	Common name	*n*	*ψ*	*p**
Cactus wren	224	0.23	1.00	Oak titmouse	4	0.01	0.86	Yellow-breasted chat	3	0.01	0.83
Cassin's kingbird	6	0.01	0.97	Orange-crowned warbler	6	0.03	0.54	Yellow warbler	10	0.02	0.79
Canyon wren	21	0.02	0.98	Phainopepla	17	0.13	0.41	Yellow-headed blackbird	2	0.02	0.59
Cedar waxwing	1	0.03	0.45	Pinyon jay	2	0.01	0.66	Yellow-rumped warbler	22	0.14	0.29
Chipping sparrow	1	0.03	0.42	Pine siskin	3	0.09	0.26				

thinned by 50 and used uninformative priors (model code presented in Appendix S2). We assessed model convergence using the Gelman-Rubin statistic, where values <1.1 indicated convergence (Gelman, Carlin, Stern, & Rubin, 2004).

To estimate and map species-specific occupancy probabilities and mammal, songbird and overall (i.e., mammal and songbird) richness, we extrapolated our model results to the entirety of California's Mojave Desert at a 1 km^2 scale. We used these model-based inferences, which rely on covariate associations, to help ensure that estimates of occupancy and richness were representative of the entire region and not just locations surveyed (Gregoire, 1998). To do this, we overlaid a 1 km^2 grid and calculated covariate values at the centre point of each grid cell. During each iteration, the model produced intercept, community-level beta and species-specific beta estimates. We used these estimates and our covariate values to generate species- and grid-specific occupancy probabilities during iteration *x*. We repeated this process for each model iteration and used these values to generate probability distributions representing species and grid-specific occupancy probabilities. Lastly, during each iteration we also summed occupancy values for mammal species, songbird species and all species to generate probability distributions representing grid-specific mammal, songbird and overall richness.

2.5 | Land designations and species richness

We used the Desert Renewable Energy Conservation Plan (DRECP, 2016) to assign five land designations: federally protected areas, conservation planning areas, recreation management areas, military land and areas that are potential sites for renewable energy development. We classified federally protected areas (i.e., National Parks, Wilderness Areas, California Desert National Conservation Lands, and BLM Areas of Critical Environmental Concern) and conservation planning areas (i.e., private lands and non-federal public lands that are a conservation priority) as protected land. We classified recreation management areas, military land and potential development sites (i.e., areas identified as open to renewable energy development in the BLM's 2016 Record of Decision regarding the DRECP) as unprotected land. Next, for our estimates of mammal, songbird and overall richness, we partitioned high-richness areas from low-richness areas using median richness values. Among the relative high-richness areas, we quantified the per cent of these areas that fell within each land designation and within protected versus unprotected land.

2.6 | Occupancy and richness projections

To forecast modelled occupancy and richness estimates, we used 2040–2069 temperature projections from the BCM (California Landscape Conservation Cooperative, 2014) and 2055 land use and land cover projections from USGS (Sleeter et al., 2017). The distributions of pinyon-juniper woodlands and free water will also likely change, but projections for these variables were not available. Consequently, we used their current values in our occupancy forecasts. For temperature, we overlaid three future scenarios for maximum monthly temperature under General Circulation Model (GCM) CMIP-5 and representative concentration pathway (RCP) 2.6 (Appendix S3). We then calculated mean maximum temperature values under RCP2.6 for each 270-m pixel and extracted values for the centre point of each 1 km^2 grid cell. We repeated this process for future scenarios under RCP4.5 (n = 2) and RCP8.5 (n = 5; Appendix S3). The selected RCPs include mitigation scenarios leading to very low (RCP2.6), medium (RCP4.5) and very high (RCP8.5) baseline emissions of greenhouse gases and air pollutants (see Van Vuuren et al., 2011 for details). For land use, we used the projection based on a mid-level human population growth rate and remeasured distances to urban development.

To forecast occupancy probabilities and mammal, songbird and overall richness in 2040–2069, we replaced grid-specific values for distance to developed area and temperature with their projected values. We then repeated the process described previously for generating probability distributions representing species and grid-specific occupancy probabilities, and grid-specific estimates of mammal, songbird and overall richness. Given we had three projected temperature values (i.e., from RCP2.6, 4.5, and 8.5), we also had three forecasted estimates of occupancy and richness. Lastly, using median values from 2016, we mapped areas predicted to have high richness in 2040–2069 under each of the future climate scenarios and determined the per cent of these areas that fell within each land use designation and within protected versus unprotected land.

3 | RESULTS

3.1 | Multispecies occupancy models

We photographed 15 mammalian species (>0.5 kg) during our 7,107 camera trap nights and recorded 68 songbird species in our 1,899 5-min acoustic recordings (Table 1). Black-tailed jackrabbit (*Lepus californicus*; $\psi = 0.70$), kit fox (*Vulpes macrotis*; $\psi = 0.41$), black-throated sparrow (*Amphispiza bilineata*; $\psi = 0.56$) and white-crowned sparrow (*Zonotrichia leucophrys*; $\psi = 0.50$) had the highest estimated occupancies (Table 1; Figure 2). Many species, conversely, had low estimates of occupancy due to their limited numbers of detections (Table 1; Figure 2). Detection probabilities tended to have a quadratic relationship with Julian day for both the mammal community and the songbird community (Table 2; Appendix S4). Further, we were more likely to detect songbirds in areas with a large human footprint but low level of background noise (Table 2; Appendix S4). Mean richness estimates at sampling sites ranged from 1–10 mammal species ($\bar{x} = 2.3$), 2–32 songbird species ($\bar{x} = 6.8$) and 4–62 species overall ($\bar{x} = 9.1$). Grid-specific estimates of mammal and songbird richness were highly correlated ($r = 0.95$) with modelled richness being greatest in the higher elevation regions, such as within the Mojave National Preserve on the eastern border of the state, for both taxonomic groups (Figure 3c,d).

Of the covariates we included in our models, maximum temperature had the greatest influence on community-level occupancy for both mammals and songbirds, with occupancy tending to decrease as maximum temperatures increased (Table 2). This negative relationship was also evident at the species level for 6 mammal and 25 songbird species (Table 2; Appendix S4). The kit fox and black-tailed gnatcatcher (*Polioptila melanura*) were the only detected species more likely to occupy sites with relatively high maximum temperatures (Appendix S4). Community-level occupancy was also influenced by proximity to pinyon-juniper woodlands, with the occupancy of mammal and songbird species tending to increase closer to woodlands (Table 2). Songbirds like the Bewick's wren (*Thryomanes bewickii*) and Crissal thrasher (*Toxostoma crissale*), and mammal species like the bobcat (*Lynx rufus*) and mule deer (*Odocoileus hemionus*) also had strong, negative relationships with distance to pinyon-juniper woodlands at the species level (Appendix S4). The species-specific influence of slope was variable, where species like the grey fox (*Urocyon cinereoargenteus*) and rock wren (*Salpinctes obsoletus*) were more likely to occupy steeper areas, while species like the coyote (*Canis latrans*) and horned lark (*Eremophila alpestris*) were more likely to occupy flatter areas (Table 2; Appendix S4). Distance to water had a stronger influence on the songbird community than the mammalian, with songbird occupancy tending to increase closer to natural water sources (Table 2; Appendix S4). Lastly, distance from a developed area had a weak influence at the community level on both mammals and songbirds, but had a strong negative influence on six songbird species (e.g., Bell's sparrow—*Artemisiospiza belli*) and a strong positive influence on two songbird species (e.g., Crissal thrasher; Table 2; Appendix S4).

3.2 | Land designations and species richness

The most prevalent land designation in the study region was federally protected areas (27,679 km^2), followed by recreation management areas (10,775 km^2), military land (9,908 km^2), conservation planning areas (1,672 km^2) and potential sites for renewable energy development (933 km^2; Figure 1). Thus, more land was protected (58%) than unprotected. For each richness measure (i.e., mammals, songbirds and overall), over 50% of the area classified as having a high value (i.e., grid value > median value) fell within land currently designated as protected (Table 3). Among the specific land designations, federally protected areas encompassed the greatest proportion of high-richness areas, followed by military lands (Table 3). Land designated for energy development encompassed 2% and 3% of high-richness areas for mammals and songbirds, respectively (Table 3).

3.3 | Occupancy and richness projections

Maximum monthly temperatures in the study area were projected to increase by an average of 1.19, 2.35 and 2.98°C under RCP2.6, 4.5 and 8.5 future scenarios, respectively, whereas mean distance to urban development was projected to decrease by just 254 m on average. These forecasted changes, namely the increase in maximum temperature, resulted in decreased estimates of occupancy from 2016 to 2040–2069 for most species (Figure 2; Appendix S5; example displayed in Figure 3a). Kit fox, ash-throated flycatcher (*Myiarchus cinerascens*), black-tailed gnatcatcher and verdin (*Auriparus flaviceps*) were among the limited number of species projected to increase in occupancy (Figures 2 and 3b; Appendix S5). We note, however, that projected occupancy estimates' 90% credible intervals overlapped current means for most species (Figure 2; Appendix S5). Some of the species that showed a statistically significant decline in projected occupancy included mule deer and black-throated sparrow under all RCP scenarios, Audubon's cottontail (*Sylvilagus audubonii*), house finch (*Haemorhous mexicanus*), cactus wren (*Campylorhynchus brunneicapillus*), Bell's sparrow, rock wren and Scott's oriole (*Icterus parisorum*) under RCP4.5 and 8.5 scenarios, and badger (*Taxidea taxus*), bobcat (*L. rufus*), Crissal thrasher and ash-throated flycatcher under the RCP8.5 scenarios (Figure 2; Appendix S5). Regarding species richness, we again found that grid-specific projections of mammal and songbird richness were highly correlated. We projected declines in overall species richness that ranged from an average of 2.5% under RCP2.6 to 19.8% under RCP8.5 (Figure 3).

For all richness measures and for all future temperature scenarios, coverage of land designated as having high value decreased substantially across the Mojave Desert from 2016 to 2040–2069 (Table 3). Similar to current modelled richness, the majority of these high value areas fell within land designated as protected, followed by recreation management areas (Table 3). Lastly, we projected

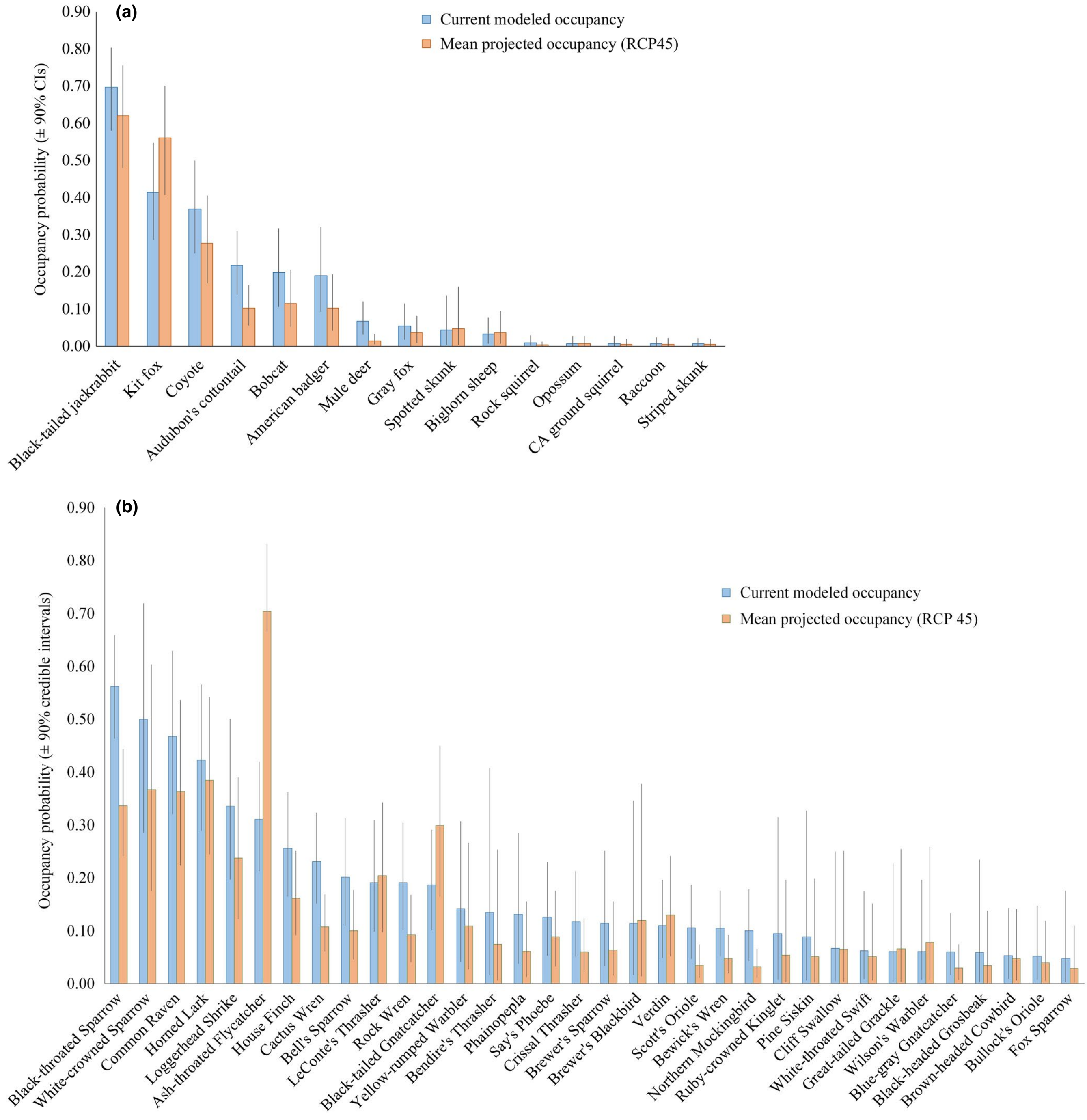

FIGURE 2 Mean estimated occupancy values, and 90% credible intervals, for mammal (a) and songbird (restricted to songbirds with occupancy estimates >0.05) (b) species across the Mojave Desert of California, 2016. We provide estimates for the current year, 2016, and forecast estimates for the years 2040–2069 using land use projections from the United States Geological Survey and maximum monthly temperatures projected under General Circulation Model CMIP-5 and representative concentration pathways (RCP) 4.5 (see Appendix S5 for occupancy projections under RCP2.6 and RCP8.5 future scenarios)

that 43% (337 km^2), 20% (159 km^2) and 14% (108 km^2) of land designated for renewable energy development, 27% (2,760 km^2), 9% (884 km^2) and 4% (409 km^2) of land designated for military, and 24% (2,709 km^2), 14% (1,585 km^2) and 10% (1,107 km^2) of land designated for recreation would be of high value to mammals and/or songbirds under RCP2.6, 4.5 and 8.5 future scenarios respectively km^2 (Figure 4; Appendix S6).

4 | DISCUSSION

We used remote camera traps and ARUs to amass spatially explicit detection–non-detection data and generate baseline estimates of occupancy for 15 mammal and 68 songbird species across the Mojave Desert in California. Such fine-scale multi-taxa data have been unavailable for this region, despite being vitally needed by

TABLE 2 Mean ($\bar{x}$) and 90% credible interval estimates for the community-level hyper-parameters hypothesized to influence the probability of occupancy and detection of terrestrial mammal species and songbird species in the Mojave Desert of California, 2016, and the number of significant species-specific responses (i.e., 90% CI did not overlap 0.0; Appendix S4)

	Mammals				Birds			
	Community		Spp.		Community		Spp.	
	$\bar{x}$	90% CI	+	−	$\bar{x}$	90% CI	+	−
Occupancy covariates								
Dist. water	−0.08	−0.315 to 0.123	0	0	−0.45	−0.686 to −0.239	4	12
Slope	−0.15	−0.641 to 0.307	3	4	−0.23	−0.388 to −0.081	2	10
Max temp.	−0.59	−1.067 to −0.107	1	6	−0.61	−0.814 to −0.416	1	25
Dist. develop	0.01	−0.198 to 0.203	0	0	−0.06	−0.217 to 0.083	2	6
Dist. woodland	−0.33	−0.705 to −0.038	0	3	−0.31	−0.523 to −0.180	1	11
Detection covariates								
Human footprint	0.14	−0.103 to 0.366	4	1	0.26	0.122–0.396	13	1
Julian day	0.72	0.250–1.172	0	3	1.74	1.153–2.373	66	0
Julian day^2	−0.53	−0.972 to −0.062	0	5	−2.07	−2.687 to −1.454	0	61
Noise					−0.17	−0.288 to −0.055	0	11

scientists, resource managers and policymakers to identify population trends, to effectively mitigate large-scale ecological stressors and to make informed land use and wildlife management decisions (Ahumada et al., 2013; Pereira et al., 2013; Steenweg et al., 2017). This data deficiency, and the focus of previous monitoring efforts on a single species or several species of interest, may be attributed to technological, analytical and budgetary constraints. Recently, however, emerging technologies such as camera traps and ARUs, which are autonomously triggered to photograph a passing animal or record a vocalizing taxa, respectively, have made it possible to continuously collect information on a diversity of wildlife species with limited human presence (Aide et al., 2013; Blumstein et al., 2011; Steenweg et al., 2017). Further, analytical advances, such as multispecies hierarchical occupancy models, have made it possible to account for observation error and to integrate data across species, thus permitting composite analyses of communities and individual species (Dorazio & Royle, 2005; Iknayan et al., 2014; Zipkin et al., 2010). These advances have opened the door to monitoring initiatives extending across greater taxonomic, spatial and temporal scales, and, in so doing, have increased our capacity for making informed land use planning and biodiversity management decisions.

Our estimates of mammal and songbird richness, both current and projected, were highly correlated (*r* > 0.9). These results suggest that mammals and songbirds are similarly distributed across the region and that areas designated as being important to the conservation of one taxonomic group will likely be important to the conservation of the other. Specifically, our research shows that when the management goal is to maximize mammal and songbird occupancy, areas with cooler temperatures that are close to pinyon-juniper woodlands and a natural water source are of high conservation value in the Mojave Desert. We found mean maximum temperature negatively influenced the occupancy of mammal and songbird communities, as well as individual species (*n* = 25). These results highlight the importance of protecting areas that may act as climate refugia, such as higher elevations, shaded valleys and north facing slopes (Bachelet, Ferschweiler, Sheehan, & Strittholt, 2016; LaDochy et al., 2007; Rapacciuolo et al., 2014; Seager et al., 2007). High elevation areas (defined here as >1,500 m) encompassed only a small portion of the region, but given that elevation and species richness were positively correlated (*r* > 0.6), their protection may be of particular importance.

Mammal and bird communities were also more likely to occupy areas close to pinyon-juniper woodlands. This positive association was likely because pinyon-juniper woodlands provide vertical habitat heterogeneity and, in turn, increased availability of nest sites, food resources, cover and shade (MacArthur & MacArthur, 1961; McCain, 2009). Thus, like high elevations, pinyon-juniper woodlands may have high ecological value for mammals and birds in the region. We encourage future research to assess a broader array of vegetation communities as our analysis was limited to pinyon-juniper woodlands. Vegetation like Joshua trees and Mojave yucca (*Yucca schidigera*), for example, may also influence species' occupancy as they too provide structural height diversity and vegetation complexity (Germano & Lawhead, 1986).

Lastly, the avian community was more likely to occupy areas close to natural water sources whereas for mammals, this relationship was weak. Water is a critical resource for vertebrate populations, but in arid ecosystems like the Mojave Desert, many mammal species (e.g., kit fox and lagomorphs) have developed physiological and behavioural adaptations that minimize their need for free water (Golightly & Ohmart, 1984; Nagy, Shoemaker, & Costa, 1976). Further, mammals may be equally dependent on ephemeral water sources, which we were unable to account for in our analyses.

Projected increases in maximum temperatures, which averaged 1.19–2.98°C across the three RCP scenarios, resulted in an overall

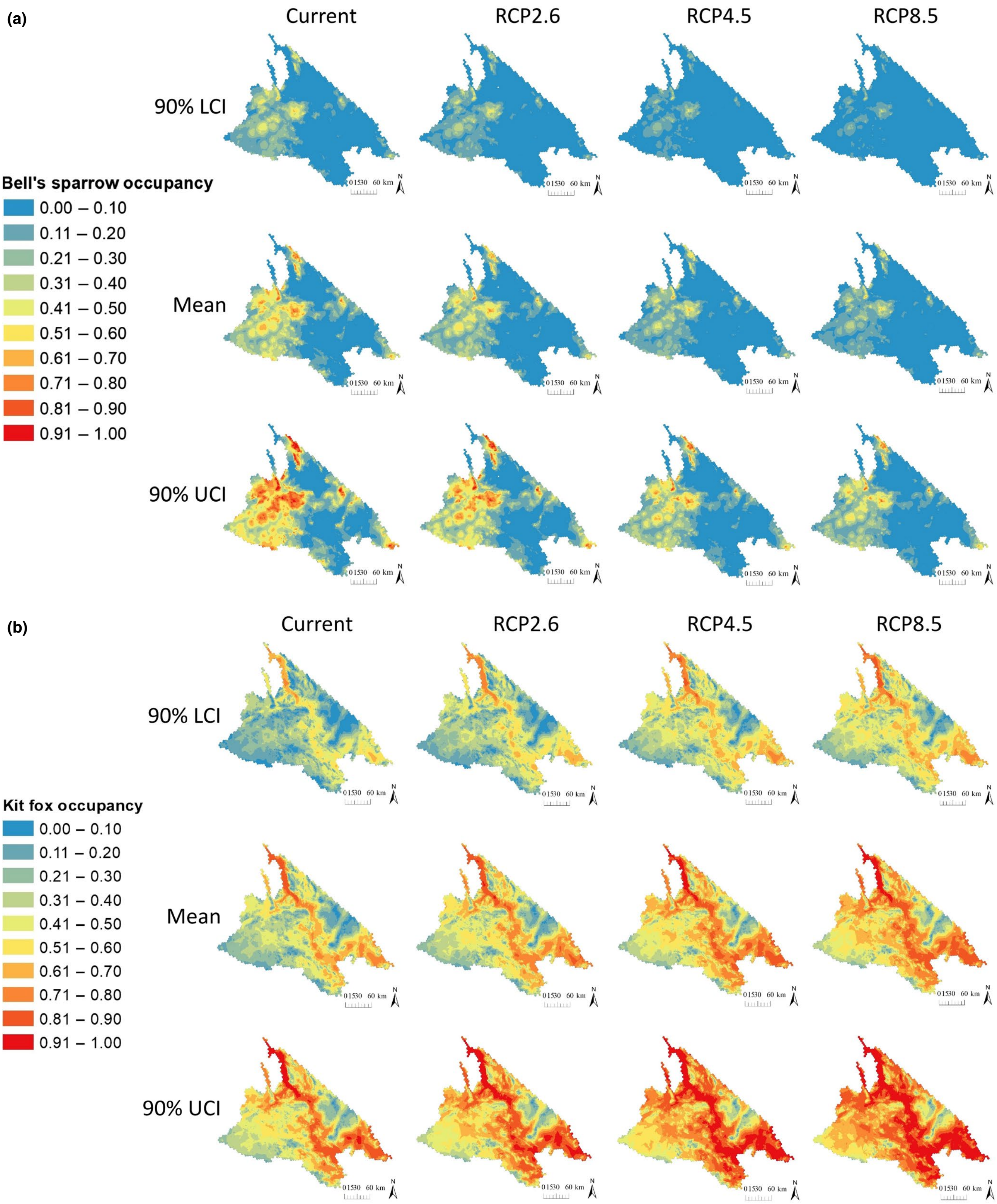

FIGURE 3 Modelled (a) Bell's Sparrow occupancy, (b) kit fox occupancy, (c) mammal richness and (d) songbird richness in the Mojave Desert of California in 2016, including 90% credible intervals (LCI = lower credible interval; UCI = upper credible interval), and projected occupancy in 2040–2069. We forecasted occupancy estimates using land use projections from United States Geological Survey and three scenarios for maximum monthly temperature in 2040–2069 under General Circulation Model CMIP-5 and representative concentration pathways (RCP) 2.6, 4.5, and 8.5

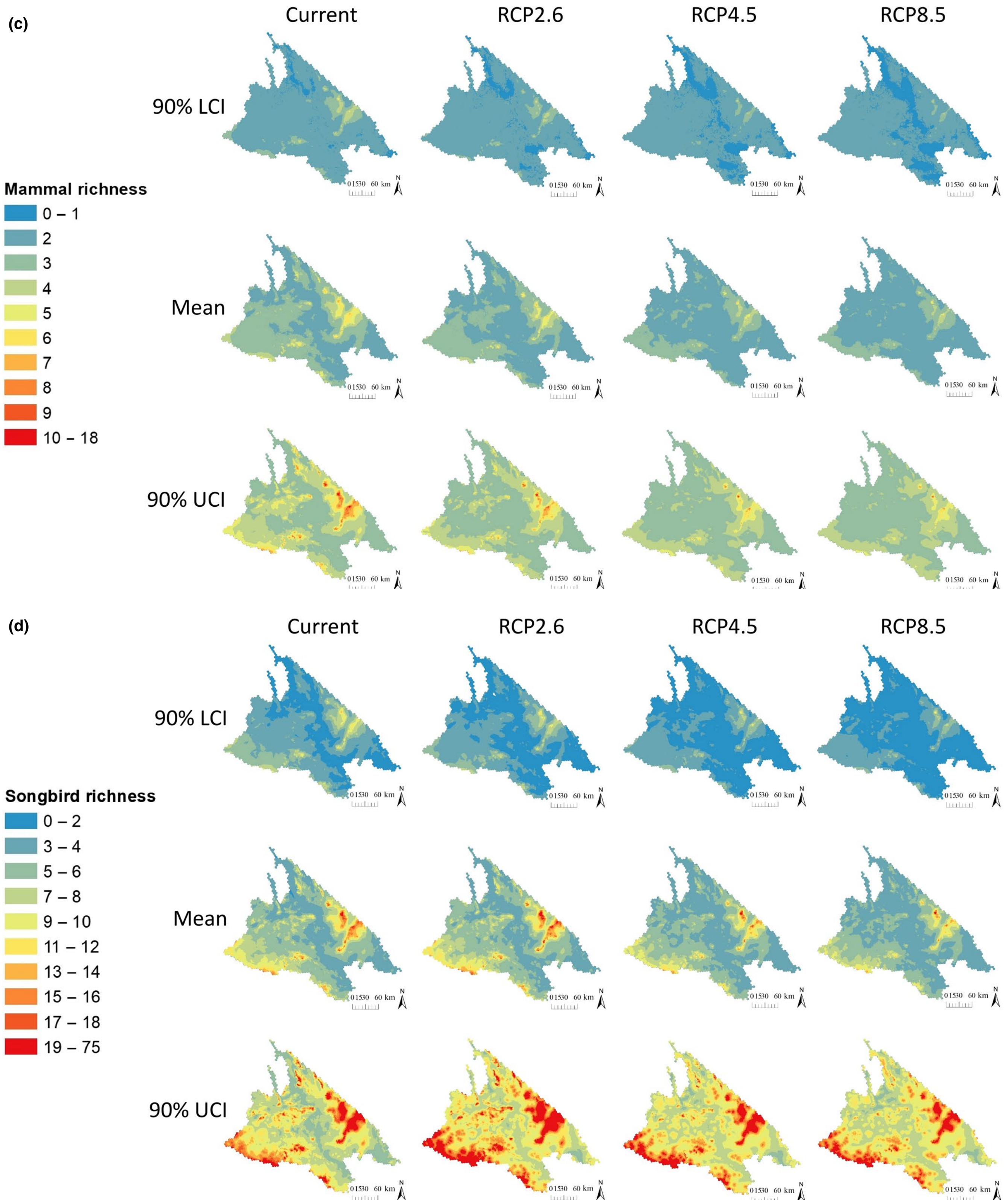

FIGURE 3 (Continued)

decline in our forecasted estimates of occupancy and richness from 2016 to 2040–2069, as well as an overall decline in the coverage of areas with high conservation value (i.e., areas where richness value was greater than 2016 median value). As expected, forecasted declines were largest under the scenario with the highest baseline emission rates (i.e., RCP8.5; Van Vuuren et al., 2011). We note, however, that confidence intervals for current and forecasted estimates often overlapped. Our results support the hypothesis that climate

TABLE 3 Per cent cover of "high" (i.e., value > median) richness areas in 2016 and in 2040–2069 in the Mojave Desert of California, where 2016 estimates of median mammal, songbird and overall richness were 2.13, 5.94 and 8.08, respectively

	Mammal richness	Avian richness	Overall richness
Overall			
% cover in Mojave			
2016	49	49	49
RCP2.6	29	28	32
RCP4.5	15	16	16
RCP8.5	11	12	12
Protected			
% federally protected			
2016	51	50	50
RCP2.6	56	52	52
RCP4.5	64	58	59
RCP8.5	69	62	63
% CPA			
2016	7	7	7
RCP2.6	7	9	5
RCP4.5	10	12	11
RCP8.5	10	13	13
Unprotected			
% energy development			
2016	2	3	3
RCP2.6	1	2	2
RCP4.5	1	2	2
RCP8.5	1	2	1
% recreation			
2016	20	19	19
RCP2.6	19	18	22
RCP4.5	19	18	19
RCP8.5	17	17	18
% military			
2016	20	21	21
RCP2.6	17	18	18
RCP4.5	6	10	10
RCP8.5	3	6	5

Note: Among the "high" richness areas, we present the per cent that falls within protected (i.e., federally protected and conservation planning areas—CPA) and unprotected (i.e., renewable energy development sites, recreation management areas, and military) land designations in 2016 and in 2040–2069. We forecasted occupancy and richness estimates using land use change projections from the United States Geological Survey and three scenarios for maximum monthly temperature in 2040–2069 under General Circulation Model CMIP-5 and representative concentration pathways (RCP) 2.6, 4.5, and 8.5.

change poses a threat to biodiversity in the Mojave Desert (Bachelet et al., 2016; Serra-Diaz et al., 2014; Walther et al., 2002). Thus, they also emphasize the need for land use and conservation planning that is informed by species-specific empirical data and designed to increase the ability of native species to persist in the face of climate change (Cameron et al., 2012; Heller & Zavaleta, 2009). We evaluated the potential impacts of increasing temperatures and human development on species distributions, but we encourage managers and land use planners to simultaneously consider projected changes in precipitation, evapotranspiration, vegetation communities and free water, all of which have also been found to influence vertebrate distributions in arid systems (Illán et al., 2014; McCreedy & van Riper, 2014).

We found 14–43, 10–24 and 4%–27% of land currently designated for renewable energy development, recreation and military activities, respectively, may be of high conservation value in the

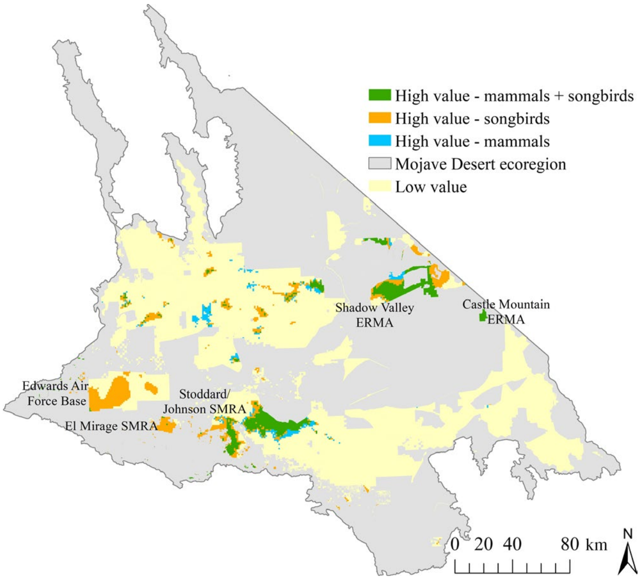

FIGURE 4 Land designated for renewable energy development, recreation and military activities in the Mojave Desert of California. We identify unprotected lands projected to be of high value to mammals, songbirds, or both mammals and songbirds in 2040–2069 (i.e., estimated mammal richness >2.13, songbird richness >5.94) and label land parcels that encompassed a large proportion of this high value habitat. We projected richness estimates using land use projections from United States Geological Survey and projected maximum monthly temperatures under General Circulation Model CMIP-5 and representative concentration pathways (RCP) 4.5 (see Appendix S6 for maps created using RCP2.6 and RCP8.5 future scenarios)

future. The Bureau of Land Management designated ~1,000 km^2 of land as open to renewable energy development (DRECP, 2016). Our results suggest that a minimum of 57% of this land may strike the balance of being suitable for renewable energy development while minimizing adverse impacts on biodiversity. Development in the remaining area, however, could negatively influence the persistence of mammal and/or songbird communities and should be considered for protection. Renewable energy benefits the long-term conservation of biodiversity by reducing climate change, but careful planning is required to ensure that future strongholds for biodiversity are not destroyed (Cameron et al., 2012; Gibson et al., 2017). While renewable energy development has garnered great attention in the Mojave Desert, it is equally, if not more important to account for pressures from recreational activities as this land use encompasses roughly 11 times the land area as energy development. For example, the Bureau of Land Management should consider limiting off-highway vehicle (OHV) activity within the 24% of recreation management areas projected to be of high conservation value under the RCP2.6 scenario including, for example, Shadow Valley, El Mirage and Castle Mountain. Recreational OHV use in California's desert southwest is increasing in popularity, likely to the detriment of flora and fauna (Cordell, Betz, Green, & Mou, 2005). Off-highway vehicle activity has been found to directly kill native plants and animals, alter animal movements, reduce reproductive and nesting success, compact soil, change water runoff patterns, and increase susceptibility to erosion (Barton & Holmes, 2007; Groom, McKinney, Ball, & Winchell, 2007; Lovich & Bainbridge, 1999). Given these negative impacts, restricting OHV use in areas projected to be of high conservation value in the future may be an important step towards minimizing conflicts between recreation interests and biodiversity conservation.

Despite sampling over 200 sites, the strength of our inferences was limited given our estimates' large 90% credible intervals, our single season of data and variability among the three future climate scenarios. To convey this uncertainty, we presented spatial projections based on 5% mean and 95% credible interval estimates for 2016 and for each of the RCP scenarios. This deviates from the common approach used in conservation science of mapping species' current and future distributions, where maps tend to represent only mean values. We note that our analyses were also restricted to linear covariate relationships, apart from Julian day, and that we did not directly evaluate potential spatial autocorrelation among our sampling sites. The spatial covariates we used in our occupancy models likely mitigated the potential issue of spatial autocorrelation, but future studies may consider using spatial occupancy models and assessing covariate relationships in greater detail by including polynomial and interaction terms (Furnas, Landers, Callas, & Matthews, 2017; Johnson, Conn, Hooten, Ray, & Pond, 2013).

An additional limitation of our research is that we frame conservation value based exclusively on the richness of songbirds and medium- to large-sized mammal species. While these taxonomic groups are important to biodiversity management, they represent only a subset of the Mojave Desert's faunal community. Managers and decision makers should expand beyond our species set and consider an array of ecological traits when determining a land parcel's conservation value. These include, for example, distributions of threatened and endangered species for which camera traps or ARUs may not be the appropriate sampling method (e.g., small-bodied species or species with limited vocalizations), protected area status, water source availability (e.g., rivers, seeps, springs), existing human infrastructure or occurrences of other flora and fauna (Hernandez et al., 2015; Randall et al., 2010). A final limitation of our study is that we do not address habitat fragmentation. Converting portions of the Mojave Desert into human-altered landscapes will create a matrix of habitat ranging from suitable to unsuitable and from permeable to impermeable (Leu et al., 2008). This fragmentation of wild desert landscapes will benefit some species but negatively influence others and should be considered during the decision-making process (Leu et al., 2008; Rodríguez-Estrella, 2007).

Climate change and anthropogenic pressures on ecosystems are accelerating within the Mojave Desert, as they are globally (Gibson et al., 2017; LaDochy et al., 2007; Leu et al., 2008; Lovich & Bainbridge, 1999; Seager et al., 2007). The result is declining biodiversity with rare species becoming rarer, geographic ranges shrinking and species becoming locally extinct (Randall et al., 2010; Sauer et al., 2017). Our research demonstrates the capacity of visual and acoustic sensors for collecting site- and species-specific data across large spatial scales that, in turn, can be used to detect biodiversity changes, to address large-scale ecological stressors and to inform proactive land management

(Blumstein et al., 2011; Cameron et al., 2012; Northrup & Wittemyer, 2013; Steenweg et al., 2017). Without this real-time empirical data on vertebrate populations, managers, researchers and policymakers are limited in their ability to design effective and efficient conservation plans. We encourage practitioners to extend beyond our snapshot in time to elucidate trends in species occupancy and richness, and to track, improve and adapt policies and management actions aimed at addressing the loss of vertebrate populations. As monitoring initiatives grow in taxonomic, spatial and temporal scope, so will our ability to surmount the tremendous challenge of maintaining and conserving biodiversity.

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DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2806394

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BIOSKETCH

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Author contribution: LNR analyzed the data and wrote the paper, BJF designed the study, DSN led field implementation of the surveys, and JSB oversaw the study. BJF, DSN, and JSB provided input on the analyses and feedback on the manuscript

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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