



# Understanding Interaction Effects of Climate Change and Fire Management on Bird Distributions through Combined Process and Habitat Models

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**Abstract:** *Avian conservation efforts must account for changes in vegetation composition and structure associated with climate change. We modeled vegetation change and the probability of occurrence of birds to project changes in winter bird distributions associated with climate change and fire management in the northern Chihuahuan Desert (southwestern U.S.A.). We simulated vegetation change in a process-based model (Landscape and Fire Simulator) in which anticipated climate change was associated with doubling of current atmospheric carbon dioxide over the next 50 years. We estimated the relative probability of bird occurrence on the basis of statistical models derived from field observations of birds and data on vegetation type, topography, and roads. We selected 3 focal species, Scaled Quail (*Callipepla squamata*), Loggerhead Shrike (*Lanius ludovicianus*), and Rock Wren (*Salpinctes obsoletus*), that had a range of probabilities of occurrence for our study area. Our simulations projected increases in relative probability of bird occurrence in shrubland and decreases in grassland and *Yucca* spp. and ocotillo (*Fouquieria splendens*) vegetation. Generally, the relative probability of occurrence of all 3 species was highest in shrubland because leaf-area index values were lower in shrubland. This high probability of occurrence likely is related to the species' use of open vegetation for foraging. Fire suppression had little effect on projected vegetation composition because as climate changed there was less fuel and burned area. Our results show that if future water limits on plant type are considered, models that incorporate spatial data may suggest how and where different species of birds may respond to vegetation changes.*

**Keywords:** climate change, conservation planning, desert birds, ecosystem modeling, fire suppression

Comprensión de los Efectos de la Interacción del Cambio Climático y el Manejo de Fuego sobre la Distribución de Aves Mediante Modelos Combinados de Procesos y Hábitat

**Resumen:** *Los esfuerzos para la conservación de aves deben considerar los cambios en la composición y estructura de la vegetación asociados con el cambio climático. Modelamos los cambios en la vegetación y la probabilidad de ocurrencia de aves para proyectar cambios en la distribución de aves en el invierno asociados con el cambio climático y el manejo de fuego en norte del Desierto Chihuahuense (suroeste de E. U. A.). Simulamos cambios en la vegetación en un modelo basado en procesos (Simulador de Paisaje y Fuego) que asoció el cambio climático esperado con el doble del dióxido de carbono atmosférico actual en los próximos 50 años. Estimamos la probabilidad relativa de la ocurrencia de aves con base en los modelos estadísticos derivados de observaciones de aves en el campo y en datos sobre el tipo de vegetación, la topografía y carreteras. Seleccionamos 3 especies focales, *Callipepla squamata*, *Lanius ludovicianus* y *Salpinctes obsoletus*,*

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que tenían una gama de probabilidades de ocurrencia en nuestra área de estudio. Nuestras simulaciones proyectaron incrementos en la probabilidad relativa de ocurrencia de aves en matorrales y decrementos en pastizales y vegetación con *Yucca* spp. y ocotillo (*Fouquieria splendens*). Generalmente, la probabilidad relativa de ocurrencia de las 3 especies fue más alta en matorrales porque los valores del índice de área del hoja fueron menores en los matorrales. Es probable que esta alta probabilidad de ocurrencia se relacione con el uso de vegetación abierta para forrajeo. La supresión de fuego tuvo poco efecto sobre la composición proyectada de la vegetación porque a medida que cambió el clima hubo menos combustible y superficie quemada. Nuestros resultados muestran que si se consideran limitaciones futuras de agua sobre las plantas, los modelos que incorporan datos espaciales pueden sugerir como y donde pueden responder a cambios en la vegetación diferentes especies de aves.

**Palabras Clave:** aves de desierto, cambio climático, modelado de ecosistema, planificación de la conservación, supresión de fuego

## Introduction

Effects of climate change, including changes in water availability, plant reproduction, and fire regime, will differ among plant species and will affect primary productivity. Potential responses of birds to climate change at local extents ( $\leq 1 \times 10^6$  m<sup>2</sup>) include changes in foraging and nesting due to changes in plant species composition and canopy structure (Marshall & Horn 1973; Pidgeon et al. 2001). At larger extents ( $> 1 \times 10^6$  m<sup>2</sup>), landscape structure (e.g., patch size, shape, and orientation) and composition (e.g., percent cover of different vegetation types) affect bird dispersal and aggregation (Gutzwiller & Barrow 2002). Recent climate change in the Chihuahuan Desert has increased the proportion of shrubs relative to grasses (Van Auken 2000). Increased proportion of shrubs is associated with decreased abundance of obligate grassland species of birds in this desert and increased species richness of breeding birds, most of which are residents (Desmond 2004).

Models of projected bird responses to climate change at continental extents incorporate environmental drivers such as temperature and precipitation via coarse-grained land-cover data (Parmesan & Yohe 2003). The bioclimatic-envelope approach, in which distributions of species are statistically modeled with meteorological variables, such as average temperature or precipitation, is robust at regional and continental extents, but is less accurate if spatial heterogeneity in these variables is great (Pearson & Dawson 2003). Vegetation patterns derived from digital information such as satellite data are moderately associated with regional bird distributions (Seoane et al. 2004). Nevertheless, maps represent vegetation as static and do not account for cycling of water and carbon, which influences vegetation composition and landscape structure.

Changes in the distribution of birds may be associated with changes in land cover and biogeochemical cycling (Jones et al. 2001). Combined models of historical land-cover change and logistic-regression models of bird occurrences derived from field observations project future abundances of individual species (e.g., Boren et al. 1997).

Contractions in the distributions of bird species are due to changes in processes that affect their habitat and can be identified through analysis of multiple scenarios of future climate change and fire disturbance (Hansen et al. 1999).

We used a mechanistic process model that simulates the relative probability of occurrence of birds on the basis of projected changes in vegetation that are functions of climate change and fire suppression. In our simulation, we assumed a doubling of atmospheric CO<sub>2</sub> from 365 to 730 ppm by 2050 (i.e., the A1F1 climate-change scenario; IPCC 2000). We selected this scenario because it represents continued growth of global economic markets, reliance on fossil fuels for energy, and of the IPCC (2000) scenarios has the highest projected increase in global temperatures by 2100. Few models of physiological responses of plants to increases in temperature and CO<sub>2</sub> exist for simulating vegetation at spatial extents at which birds are likely to respond to changes in vegetation type and biomass (Peters 2002). Fewer yet project bird responses to climate-induced vegetation change (Dormann 2007).

## Methods

The models we developed were part of a more comprehensive study on the effects of climate change and fire management in a 3600-km<sup>2</sup> area centered on Big Bend National Park (Texas, U.S.A.), which is located in the northeastern Chihuahuan Desert. Elevations range from 550 m along the Rio Grande in the south to 2388 m in the Chisos Mountains near the center of the park. The non-montane lowlands ( $< 1200$  m) are primarily composed of shrublands in which the dominant species are creosote (*Larrea tridentata*), prickly pear cactus (*Opuntia* spp.), and agave (*Agave lechuigilla*); grasslands dominated by various grama species (*Bouteloua* spp.); and communities in which the dominant species are *Yucca* spp. and ocotillo (*Fouquieria splendens*). Mexican piñon pine (*Pinus cembroides*) and red-berried juniper (*Juniperus*

*erythrocarpa*) dominate montane uplands ( $\geq 1200$  m). Mean annual precipitation is approximately 30 cm, with most precipitation occurring in August and September. Meteorological data from 1957 to 2001 show average daily temperatures range from 13.8 °C in January to 25.0 °C in July.

### Bird Surveys and Focal Species

Detailed descriptions of survey sites and methods are in Gutzwiller and Barrow (2003) and Gutzwiller et al. (2010). We surveyed birds at 70 sites (points) located on average 400 m from paved or dirt roads. Each site was at the center of a circle with a 2-km radius within which we measured topography, vegetation, and other variables. Each site was separated from all other sites by  $\geq 4$  km. We surveyed birds from December to February of 1999–2002 (3 winters) with 20-minute unlimited-distance point counts (Ralph et al. 1995). We focused on the presence and absence of Scaled Quail (*Callipepla squamata*), Loggerhead Shrike (*Lanius ludovicianus*), and Rock Wren (*Salpinctes obsoletus*). The proportion of sites at which these species were present differed considerably, which enabled us to incorporate a range of occurrence values into the analyses.

### Measurements of Vegetation and Topography

We used data from Landsat Thematic Mapper-5 (30-m resolution) from the spring of 1999 to classify land cover as shrubland, grassland, *Yucca* spp. and ocotillo, riparian vegetation, or montane forest. Based on field surveys at 152 sites in the study area, the classification had an overall accuracy of 77% (White et al. 2008). We estimated leaf-area index (LAI) for each 30-m grid cell from the satellite-derived simple ratio spectral vegetation index. The latter index was calibrated from LAI values measured in the field (near infrared to red; White et al. 1997). We derived elevation, slope, and aspect at 30-m resolution from a digital elevation model (U.S. Geological Survey 1993). We resampled all digital data to 60-m resolution.

We did not calculate the detection probability for each species, but we accounted for influences of observers and visibility as described in Gutzwiller and Barrow (2008). Two field observers collected the bird data over 3 years. To simulate these observers across the study area, we created a map of the study area at a 60-m resolution and then randomly assigned a value of 0 or 1 to each grid cell to represent the identity of these 2 observers.

We estimated visibility as the unobstructed view of an observer with at least 342° of sighting distance to 100 m. For each grid cell, we calculated the line of sight obstruction from the central cell to the 8 adjacent cells by comparing 2 topographic slopes: slope between the centers of the central cell and the adjacent cell (60 m) and slope between the central cell and the cell beyond the adjacent cell (120 m). If the slope beyond the adjacent cell

was greater than the slope between the central cell and adjacent cell, we considered the view topographically obstructed (Anile et al. 2003). We added a correction of 2 m to the elevation of the central cell to account for the average height of the standing observer. If cells adjacent to the central cell had LAI values  $>3.0$ , we assumed the line of sight was obstructed. We used this value because in our study area vegetation with LAI  $>3.0$  tended to be  $>2.0$  m tall. Comparison of modeled and observed visibility revealed a map accuracy of 67%. Mapped relative probability of bird occurrence accounted for values of visibility modified by future LAI values.

For the set of cells within the 2-km-radius circle, we calculated mean LAI and the coefficient of variation of LAI. We used the software FRAGSTATS (McGarigal & Marks 1995) to measure 6 variables for each of the circles: percent cover of shrubland, grassland, *Yucca* spp. and ocotillo, riparian vegetation, roads, and montane forest. Montane forest was absent from all but 2 of the 70 circles, so it was not included in regression modeling of bird-landscape relations. For each survey site, we derived the point elevation from a digital elevation model and recorded observer identity for each winter.

### Regression Analyses

We categorized each of the 3 species as present or absent for each site and year on the basis of point-count data. We used these data as the dependent variables in stepwise logistic-regression analyses in Proc Logistic (SAS 1999; Hosmer & Lemeshow 2000). It was not feasible for us to explicitly estimate the probability of failing to detect a species that was present at a site. Consequently, our response variable was the relative probability of occurrence. Candidate predictor variables included mean LAI, coefficient of variation of LAI, percent cover of shrubland, grassland, yucca-ocotillo, riparian vegetation, and roads; elevation, observer identity, and visibility. To reduce the probability of type II errors, we used an a priori  $\alpha$  of 0.10 for all regression analyses (Gutzwiller & Barrow 2003). To reduce the possibility of spurious relations and overfitted models, we determined which predictor variables were significantly related to the dependent variable with a sequential Bonferroni adjustment of a family-wide  $\alpha$  of 0.10 (Holm 1979; Gutzwiller & Barrow 2008). To avoid problems associated with separation, zero cell counts, collinearity, and imprecise estimates of coefficients, we assessed whether predictors in the model had large coefficients, large standard errors for the coefficients, or standard errors for the coefficients that were larger than the coefficients themselves (Hosmer & Lemeshow 2000; Gutzwiller & Barrow 2003).

We used the model deviance-to-df ratio that we obtained through Proc Genmod (SAS 1999) to assess whether models were influenced by spatial autocorrelation, outliers, or an inappropriate distributional model.

Values of this ratio close to 1.0 indicate no evidence of these problems (Allison 1999; Schabenberger & Pierce 2002). For each regression model, the  $-2\log L$  and score statistics were significant, which indicated that the set of predictors was significantly associated with occurrence; and the  $-2\log L$  statistic for each predictor was significant, indicating a particular predictor was significantly associated with occurrence (Allison 1999; Gutzwiller & Barrow 2003).

As described in Gutzwiller and Barrow (2003), we used maximum-rescaled  $R^2$  to quantify the percentage of variation in occurrence associated with the predictors and Proc Logistic (SAS 1999) to compute percent correct classification of a species' presence or absence, which indicated the model's ability to predict species occurrence for each site on the basis of the model derived from the remaining 69 sites. We did not have sufficient personnel to conduct point counts for birds across the entire study area. Therefore, it was not clear that occurrences derived from point-count data for our 70 survey sites were accurate estimates of occurrences in the entire study area. Because of this uncertainty, we used equal prior probabilities to classify whether a species was present or absent at each site (Hair et al. 1998). For model validation, we classified whether a species was present or absent at each site in terms of species occurrence by applying the conservative cut-off probability of 0.5 (probability  $\geq 0.5$ , present; probability  $< 0.5$ , absent). We considered the accuracy of classifications better than chance accuracy if the overall correct classification percentage was  $\geq 62.5\%$  (Hair et al. 1998; Gutzwiller & Barrow 2003).

For several reasons the stepwise method we used was more appropriate than a confirmatory method that infers causation and that requires a relatively small set of a priori candidate models (e.g., assessment of model selection uncertainty, Burnham & Anderson 2002). First, our simulations, which incorporated plant biology and fire behavior, accommodated only certain variables, and we were not aware of information about whether these variables were likely to drive species' occurrences. Second, because our previous research in the study area occurred during the breeding season and involved different vegetation classes with a finer spatial resolution, reliance on relations from this earlier work to identify candidate variables for our analysis here could have resulted in inappropriate models. Third, no one has studied how the landscape variables we needed to consider here may influence the occurrence of our focal species during winter. Fourth, the purpose of the regression analyses was to identify variables that would enable reasonable projections of bird distributions, not to draw inferences about mechanisms that drive species' occurrences. Under these circumstances, our stepwise approach was acceptable as an initial step (Gutzwiller & Barrow 2008) in the development of the predictive models.

## Models of Vegetation Change and Fire

We simulated vegetation change with the Landscape and Fire Simulator. This model was developed specifically for our work on climate and fire management in Big Bend National Park and calculates daily microclimate, carbon and water budgets, seed dispersal, and fire spread for functional plant types for defined grid cells (White et al. 2008). In these simulations, there were 6 representative plant types: semideciduous  $C_3$  woody shrub (e.g., *Larrea tridentata*), deciduous  $C_4$  grass (e.g., *Bouteloua ramosa*), evergreen crassulacean acid metabolism cactus (e.g., *Opuntia* spp.), deciduous  $C_3$  ocotillo (*F. splendens*), evergreen riparian  $C_3$  tree (e.g., *Tamarix ramosissima*), and evergreen montane  $C_3$  tree (e.g., *Pinus* spp.). The plant types also represented physiological types as defined by their mode of photosynthesis, persistence of foliage, and presence of woody tissue.

We used daily meteorological variables to model plant growth (Thornton & Running 1999). Plant production was modeled from models of photosynthetic pathways that respond to changes in atmospheric  $CO_2$  concentrations (White et al. 2008). In general,  $C_3$  plants respond directly to  $CO_2$  increases more than plants with  $C_4$  or crassulacean acid metabolism because they assimilate carbon into sugars more directly than non- $C_3$  species. We calculated soil moisture as the difference between evapotranspiration and infiltration with root-zone partitioning. Phenology of vegetation was based on sensitivity of each plant functional type to soil moisture and was temperature specific for each plant functional type (White et al. 2008).

Plant growth was initially estimated from net primary production (NPP):  $NPP = GPP \cdot 0.45$  (Landsberg & Waring 1997), where GPP (gross primary production) is the amount of photosynthetic assimilation of carbon into sugar. We distributed NPP to leaves, stems, storage, flowers, seeds, and roots monthly on the basis of static fractions of primary productivity. Mortality rates of plants associated with fire and annual turnover were based on an exponential decay function. We used a moving window in which seeds were distributed from the central cell to neighboring cells to model seed dispersal.

We determined the potential for fire ignition in each cell on the basis of the occurrence of meteorological conditions favorable for lightning, fuel moisture, and historical fire occurrence (Keane et al. 1996) in the study area (Moir 1982). When ignition occurred in the simulation, we modeled fire spread spatially, and fire consumed fractional amounts of vegetation and litter within each affected grid cell (Li 2000). Each grid cell's vegetation type was assigned on the basis of the dominant type of plant cover ( $> 50\%$ ). For example, if the vegetation of the simulated grid cell contained a  $C_4$  grass that covered  $> 50\%$  of the cell, the cell was categorized as grassland.

## Modeled Scenarios

We modeled the response of vegetation to climate change, increased atmospheric CO<sub>2</sub>, and fire suppression and used model outputs as inputs for modeling relative probabilities of bird occurrence. For the climate-change scenario, we calculated quarterly projected changes in temperature and precipitation on the basis of the A1F1 scenario of the Hadley HadCM3 model (Pope et al. 2000) for 1970–2050. We ran simulations for 50 years at a 60-m resolution; each scenario run required 1 month of computational time. We constructed daily meteorological data from weather conditions in random years (1957–2001) recorded at the meteorological station at Panther Junction in Big Bend National Park. For each day, we adjusted temperature and precipitation values trimonthly on the basis of HadCM3 predictions for a net increase of 3.5 °C and a total decrease of 1.5 cm in annual precipitation by 2050. Although Pope et al. (2000) derived the HadCM3 scenario temperature and precipitation projections from their original data with a 0.5° grain, the meteorological submodel in the Landscape and Fire Simulator accounted for topographic variation in meteorological conditions for this area. We assumed concentrations of CO<sub>2</sub> increased from 365 ppm to 730 ppm over 50 years and included an increase in CO<sub>2</sub> of 0.02 ppm/day. No CO<sub>2</sub> generated by fires was incorporated into the analyses. We also simulated a scenario in which we used the same randomized meteorological data without climate change or CO<sub>2</sub> increases.

We modeled the effect of fire on bird occurrence by simulating fires that were not suppressed or by simulating fire suppression. We simulated fire suppression by stopping fires >2000 ha, which is in general the maximum area in which fire fighters can contain fires in Big Bend National Park for a given day.

## Relative Probability of Occurrence of Birds

For each scenario, we calculated and mapped the relative probability of occurrence of each species of bird for each grid cell on the basis of the variables derived for the logistic regression models among all modeled scenarios for 3 years (Table 1) and projected vegetation type and LAI. From the Landscape and Fire Simulator outputs, we calculated mean LAI and coefficient of variation of LAI for all cells, percent cover of shrubland, grassland, *Yucca* spp. and ocotillo, and riparian vegetation within a 2-km radius of each simulation cell. We calculated percent cover of roads within a 2-km radius of each simulation cell with digital transportation data (U.S. Geological Survey 1:100,000 digital line graph data) for the study area. Point values of elevation were derived from a digital elevation model (U.S. Geological Survey 1993 1:24,000 data) and modeled observer identity and visibility were taken from our derived maps. We calculated the mean vegetation cover, LAI, and relative probability of occur-

rence for each bird species for the entire study area to assess potential future trends. We created images of only the current, climate change, and no climate change, no fire-suppression scenarios, which represent the extremes of our projected distributions.

## Effects of Climate Change and Fire Suppression on the Relative Probability of Occurrence

For every simulation cell, we evaluated climate-change and fire-suppression effects on the relative probability of occurrence on the basis of changes in relative probability of occurrence ( $P$ ) among scenarios:

$$\Delta P\% = \left( \frac{P_B - P_A}{P_A} \right) 100\%,$$

where  $B$  is the treatment scenario and  $A$  is the reference scenario. For example, to test only the effect of climate change on the relative probability of occurrence of a given species, relative probability of occurrence for the scenario with climate change and no fire suppression was the treatment scenario, and the relative probability of occurrence for no climate change and no fire suppression was the reference value. The numbers of cells for which values of the relative probability of occurrence increased or decreased by more than 10% were counted in each scenario comparison. We selected the 10% threshold to reduce biases associated with random error in maps and models. For each grid, we used a nonparametric sign test and a  $\chi^2$  statistic ( $df = 1$ ) to evaluate whether changes in the proportion of occupied cells were significant (Hays 1988; SPSS, Chicago, Illinois). For each of the 3 years for which we obtained values of relative probability of bird occurrence, we compared effect of climate change with and without fire suppression and no climate change with fire suppression. We evaluated the test results with a standard Bonferroni adjustment of  $\alpha = 0.05$  for the 3 comparisons.

## Results

### Bird Occurrence and Bird-Landscape Regression Models

Birds occurred at 33–46% (Scaled Quail), 66–74% (Loggerhead Shrike), and 76–86% (Rock Wren) of sites. All the regression coefficients were relatively small (Table 1), and the standard errors of the coefficients were smaller than the coefficients themselves, which indicates that the results were not affected by separation, zero cell counts, collinearity, or imprecise coefficients. The magnitudes of coefficients and their standard errors were not affected adversely by unusually small or large measurement units or data values for the response or predictor variables. For all models, ratios of deviance to  $df$  were close to 1.0 (Table 1). Maximum-rescaled  $R^2$  values (Table 1) indicated that from 19% to 43% of the variation in species' occurrences was associated with the predictor variables.

**Table 1. Regression models for 3 bird species and model fit and predictive ability.**

Bird species and year	Model*	Deviance: df	Maximum-rescaled R <sup>2</sup> (%)	Presences classified correctly (%)	Absences classified correctly (%)	Overall correct classification (%)
<b>Scaled Quail</b>						
<i>(Callipepla squamata)</i>						
1999-2000	-5.717 + 0.255(YUCOCO)+0.006(ELEV)	1.1	38	63	76	70
2000-2001	-2.992 - 3.125(LAICV)+0.056(SHRUBL) - 1.870(OBSN)	1.1	41	64	86	77
2001-2002	-7.409 - 3.984(LAIM)+0.214(YUCOCO)+0.010(ELEV)	1.0	37	52	87	76
<b>Loggerhead Shrike</b>						
<i>(Lanius ludovicianus)</i>						
1999-2000	2.518 - 2.461(LAICV) - 1.119(OBSN)	1.1	24	90	23	69
2000-2001	-3.114 + 0.050(SHRUBL)+1.520(VISIB) - 1.449(OBSN)	1.1	32	80	58	73
2001-2002	1.649 - 1.442(LAIM)+1.583(VISIB)	1.1	19	98	6	74
<b>Rock Wren</b>						
<i>(Salpinctes obsoletus)</i>						
1999-2000	2.676 - 0.051(GRASSL) - 0.442(RIPAR)	0.8	22	97	9	83
2000-2001	2.874 - 0.068(GRASSL)	0.7	22	97	10	84
2001-2002	2.747 - 0.086(GRASSL)+0.484(YUCOCO) - 1.747(OBSN)	0.8	43	96	41	83

\*Abbreviations: LAIM, mean leaf area index; LAICV, coefficient of variation of leaf area index; GRASSL, percent cover of grassland within 2-km radius of the survey site; YUCOCO, percent cover of yucca-ocotillo; SHRUBL, percent cover of shrubland; RIPAR, percent cover of riparian vegetation; VISIB, visibility; OBSN, observer identity; ELEV, elevation in meters.

The correct classification percentage for absence dominated the overall correct classification percentage for Scaled Quail, whereas the correct classification percentage for presence dominated the overall correct classification percentages for Loggerhead Shrike and Rock Wren (Table 1). The overall correct classification percentage for the models ranged from 69% to 84% (Table 1), which indicates the predictive accuracy of the models was relatively high and greater than chance accuracy.

### Vegetation Model

Our models projected an overall reduction in LAI for the shrubland, grassland, and *Yucca* spp. and ocotillo vegetation types with little effect of fire suppression (Fig. 1). Grassland and *Yucca* spp. and ocotillo LAI decreased more than shrubland LAI; therefore, vegetation in the climate-change scenarios was dominated by shrublands. Leaf area index was higher in scenarios without than with climate change. On the basis of total site LAI, although the uplands remained dominated by trees in all future scenarios, shrubs dominated much of the landscape in the climate-change scenarios (Fig. 1). Fire suppression reduced the amount of area burned for both climate scenarios. The cumulative percentage of the study area burned in the climate-change scenarios with no fire and with fire suppression were 3.05% and 2.95%, respectively. The cumulative percentage of the study area burned in the

scenarios of no climate change with no fire and fire suppression were 3.15% and 3.10%, respectively.

### Relative Probabilities of Occurrence of Birds

The projected relative probability of occurrence of the 3 bird species was variable and skewed (Table 2). Individual species generally had higher relative probability of occurrence values in scenarios with climate change than in scenarios without climate change. Fire suppression had little influence on the relative probability of occurrence for all species. In addition, the response of species' relative probabilities of occurrence to topographic and vegetation variables, and scenarios varied geographically (Figs. 2a-c).

The projected relative probability of occurrence of Scaled Quail was the lowest of the 3 species and ranged from a mean of 0.23 (SD 0.28) to 0.53 (0.28) (Table 2). Of the annual models, the projected relative probability of occurrence for 1999-2000 and 2000-2001 decreased for all scenarios. Only the 2001-2002 model had higher mean relative probability of occurrence values for both climate-change scenarios (0.44 [0.31]); relative to the current scenario (0.38 [0.30]). The average relative probability of occurrence for all years was not different between current (0.44 [0.23]) and climate-change scenarios (both 0.44 [0.22]); however, relative probabilities of occurrence in both scenarios without climate change were lower (0.38

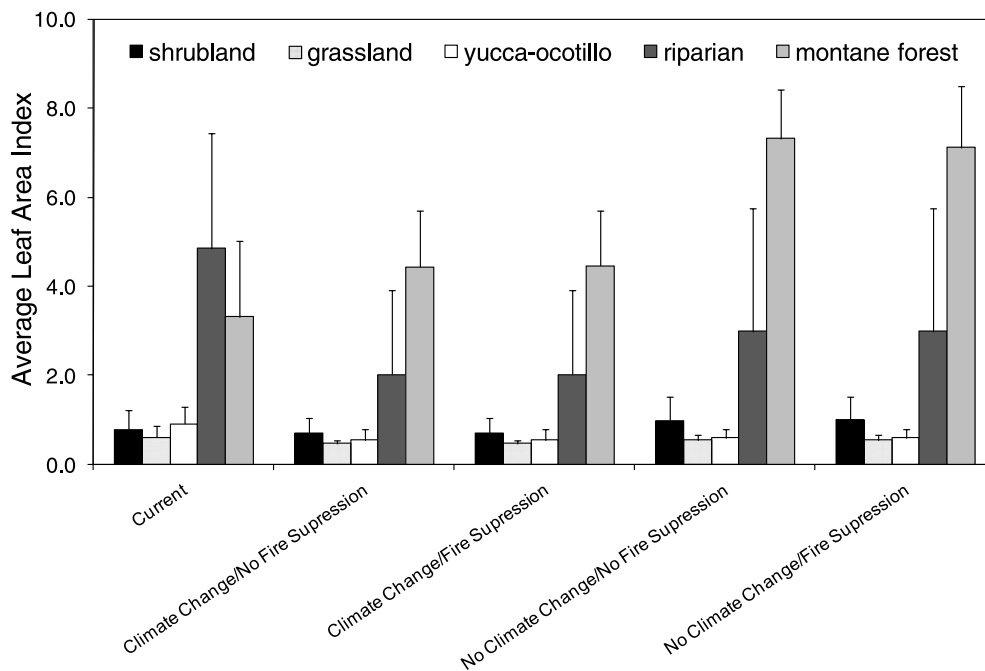


Figure 1. Average leaf area index of different vegetation types associated with current climate (derived from analysis of satellite imagery) and the following scenarios (derived from modeling): climate change and no fire suppression, climate change and fire suppression, no climate change and no fire suppression, and no climate change and fire suppression. Error bars are 1 SD.

[0.19]) than with climate change (0.44 [0.22]). Projected relative probabilities of occurrence for Scaled Quail were lower than projected relative probabilities of occurrence of the other 2 species (Fig. 2a). In areas with elevation over 1200 m, such as the Chisos Mountains, projected relative probability of occurrence of Scaled Quail changed more under the climate-change scenario than under the

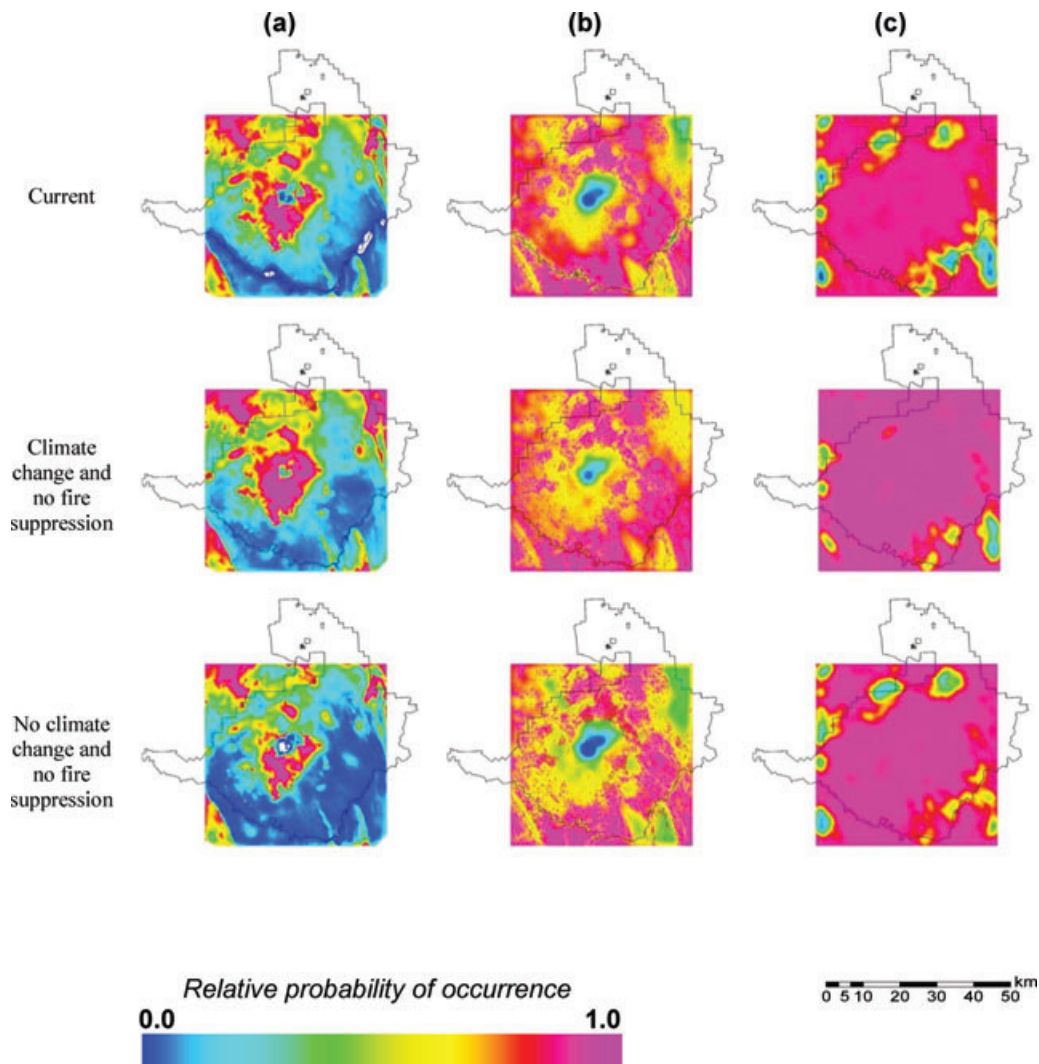
current scenario and the scenario without climate change or the fire-suppression scenario (Fig. 2a).

Mean values of projected relative probability of occurrence ranged from 0.62 (SD 0.18) to 0.74 (0.15) for Loggerhead Shrike (Table 2). Similar to Scaled Quail, the projected relative probabilities of occurrence for 1999–2000 and 2000–2001 were lower than the current

Table 2. Mean simulated relative probability of occurrence for each bird species given current conditions and in the 4 climate-change and fire scenarios\*.

Bird species and year	Scenario				
	current (SD)	climate change, no fire suppression (SD)	climate change, fire suppression (SD)	no climate change, no fire suppression (SD)	no climate change, fire suppression (SD)
<b>Scaled Quail</b>					
1999–2000	0.53 (0.28)	0.52 (0.28)	0.52 (0.28)	0.52 (0.28)	0.52 (0.28)
2000–2001	0.42 (0.28)	0.39 (0.26)	0.39 (0.26)	0.34 (0.26)	0.34 (0.26)
2001–2002	0.38 (0.30)	0.41 (0.31)	0.41 (0.32)	0.23 (0.28)	0.27 (0.29)
Average	0.44 (0.23)	0.44 (0.22)	0.44 (0.22)	0.38 (0.19)	0.38 (0.19)
<b>Loggerhead Shrike</b>					
1999–2000	0.68 (0.19)	0.64 (0.17)	0.64 (0.17)	0.62 (0.18)	0.63 (0.18)
2000–2001	0.72 (0.24)	0.69 (0.22)	0.69 (0.22)	0.66 (0.24)	0.66 (0.24)
2001–2002	0.72 (0.18)	0.74 (0.15)	0.74 (0.15)	0.67 (0.19)	0.67 (0.19)
Average	0.67 (0.14)	0.69 (0.13)	0.69 (0.13)	0.65 (0.14)	0.65 (0.14)
<b>Rock Wren</b>					
1999–2000	0.84 (0.16)	0.88 (0.12)	0.88 (0.12)	0.87 (0.15)	0.85 (0.15)
2000–2001	0.86 (0.16)	0.90 (0.11)	0.90 (0.11)	0.87 (0.15)	0.87 (0.15)
2001–2002	0.78 (0.24)	0.82 (0.19)	0.82 (0.19)	0.77 (0.24)	0.77 (0.24)
Average	0.82 (0.17)	0.87 (0.12)	0.87 (0.12)	0.84 (0.17)	0.83 (0.16)

\*Model averages and standard deviations are derived from cumulative simulation cells for each year.



**Figure 2.** Projected distribution of the relative probability of occurrence of (a) Scaled Quail, (b) Loggerhead Shrike, and (c) Rock Wren under current climate and the following climate-change scenarios: climate change and no fire suppression and no climate change and no fire suppression in Big Bend National Park, Texas (U.S.A.). Each pixel is  $60 \times 60$  m.

scenario. The relative probability of occurrence for 2001–2002 was higher for both climate-change scenarios (mean [SD] = 0.74 [0.15]) than for the current scenario (0.72 [0.18]). Averaged relative probability of occurrence for the climate-change scenarios was higher (0.69 [0.13]) than for the current scenario (0.67 [0.13]) and lowest for the scenarios without climate change (0.65 [0.14]). For this species the scenario of climate change without fire suppression was associated with the highest relative probability of occurrence, especially in the Chisos Mountains (Fig. 2b). The scenario of no climate change or fire suppression was associated with lower relative probability of occurrence compared with the current scenario and the scenario of climate change without fire suppression (Fig. 2b).

The Rock Wren had the highest mean relative probability of occurrence (range 0.77 [SD 0.24] to 0.90 [0.11]) (Table 2). Unlike the other species, the relative probability of occurrence of Rock Wren in most of the annual models was higher for scenarios with and without climate change than for the current scenario. Only the no-climate-change scenario for 2001–2002 was associated with slightly lower relative probability of occurrence (0.77 [0.24]) for Rock Wrens than the current scenario (0.78 [0.24]). Projected distributions included isolated areas of potential change in the northern region of the study area (Fig. 2c). Under all scenarios, however, areas with the lowest relative probability of occurrence were located along the southern boundary of the study area within the Rio Grande Valley.



**Table 3.** Percentage of the study area for which change in the relative probability of occurrence of each species was >10% in each climate-change scenario relative to the no climate change and no fire suppression scenarios.

Bird species and year	Scenario		
	climate change, no fire	climate change, fire	no climate change, no fire
<b>Scaled Quail</b>			
1999-2000	0.0	0.0	-2.0
2000-2001	26.0*	26.0*	-2.0
2001-2002	96.0*	96.0*	0.0
<b>Loggerhead Shrike</b>			
1999-2000	2.0	2.0	-4.0
2000-2001	20.0*	20.0*	0.0
2001-2002	52.0*	52.0*	0.0
<b>Rock Wren</b>			
1999-2000	0.0	0.0	-6.0
2000-2001	12.0*	12.0*	0.0
2001-2002	20.0*	18.0*	-2.0

\*Significant difference between scenarios ( $p < 0.017$ ). A standard Bonferroni reduction of the  $\alpha$  level (0.05) for this test was based on 3 comparisons.

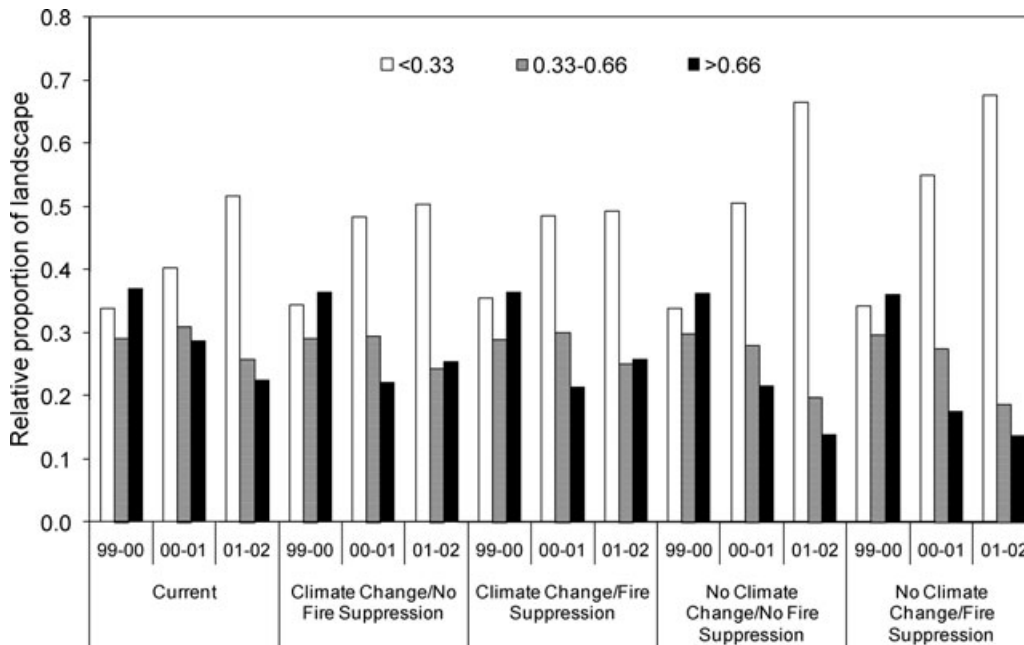
The percentage of the study area with significant (>10%) changes in relative probability of occurrence ranged from 12% to 96% (Table 3). The climate-change scenarios affected all species. Nevertheless, we detected no effect for the scenario of no climate change with fire suppression. In addition, the relative probability of occurrence for all species increased significantly for the

scenarios of climate change with and without fire suppression for 2000-2001 and 2001-2002.

### Discussion

Our results show potential influences of climate change on bird occurrence on the basis of a model that uses the physiological response of vegetation to climate and fire management. We identified ecological factors that may influence the occurrence of birds (Seoane et al. 2005). For example, LAI often explained the relative probability of occurrence of Scaled Quail and Loggerhead Shrike. Because LAI is related to canopy cover and primary productivity, for these species it may indicate the availability of shelter and food.

The association between decreased LAI and increased relative probability of occurrence of Scaled Quail may be due to the species' improved ability to escape predators where the ground is bare (Saiwana et al. 1998). The bird's association with shrub-dominated areas with bare rocks, where they can view and capture prey more effectively (Wiens & Rotenberry 1981), may explain the association between LAI and relative probability of occurrence for Loggerhead Shrike. Variation in LAI may have changed visibility of birds. Nevertheless, detection of birds in the northern Chihuahuan Desert does not appear to differ appreciably in vegetation of different heights and biomass (Pidgeon et al. 2001). Thus, associations of LAI with projected relative probability of occurrence were likely due to bird ecology rather than unequal detection probability.



**Figure 3.** Modeled relative probability of occurrence of Scaled Quail for each of 3 years (1999-2002) associated with current climate and with climate change and fire scenarios. Bars are the relative proportion of the study area in which relative probabilities of occurrence were <0.33, 0.33-0.66, and  $\geq 0.67$ .

Our models did not directly reflect physiological responses of birds to climate change or behavior related to nest-site selection or territory maintenance. Nevertheless, the composition and structure of plant communities (e.g., LAD) were affected indirectly by temperature and water availability. Therefore, if the bird species responded to these variables as represented by the statistical models (Table 1), physiological drivers may indirectly affect them.

Projected relative probabilities of bird occurrence did not account for variance in modeled estimates of statistical parameters and likely influenced the statistical significance of the scenario results (Table 3). We did not vary the parameters in the bird models because computational requirements were for 1,000,000 simulation grid cells. For the significance tests, we used spatial variance of projected relative probability of occurrence as a substitute for point variance.

The climate-change scenario we selected is one of several projections from global circulation models. The Landscape and Fire Simulator projected an increase in shrubland cover in this climate-change scenario. A recent model by Peters (2002) shows increased grassland cover for the northern Chihuahuan Desert and an increase in annual precipitation of 6.6 cm for the same time period.

The annual variability in distributions of the relative probability of occurrence values for Scaled Quail across current and future scenarios (Fig. 3) was due to our use of different landscape variables in the Scaled Quail model for each year and the different vegetation characteristics simulated from each scenario. Annual fluctuations in values of the variables used in the models could be used to assess sensitivity of this species to extirpation.

Combined models such as those presented here can identify species that are potentially sensitive to landscape changes (Currie 2001). This process is compatible with the Dynamic Habitat and Population Analysis approach (Hansen et al. 1999) and improves on efforts to define habitats on the basis of results of ecosystem-process modeling and landscape analyses. The multiple-year approach we used can provide a more robust projection of species distributions (Araújo & New 2007). Uncertainties exist in our analysis. There was annual variation in statistical models, uncertainty in the statistical model parameters, and decadal variation in the composition of vegetation that may influence interpretation of the occurrence of birds in an area.

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