

Between a rock and a hard place: the impacts of climate change and housing development on breeding birds in California

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Abstract Although the effects of climate change on species distributions have received considerable attention, land-use change continues to threaten wildlife by contributing to habitat loss and degradation. We compared projected spatial impacts of climate change and housing development across a range of housing densities on California's birds to evaluate the relative potential impacts of each. We used species-distribution models in concert with current and future climate projections and spatially explicit housing-develop-

ment density projections in California. We compared their potential influence on the distributions of 64 focal bird species representing six major vegetation communities. Averaged across GCMs, species responding positively to climate change were projected to gain 253,890 km² and species responding negatively were projected to lose 335,640 km². Development accounted for 32 % of the overall reductions in projected species distributions. In terms of land area, suburban and exurban development accounted for the largest portion of land-use impacts on species' distributions. Areas in which climatic suitability and housing density were both projected to increase were concentrated along the foothills of the Sierra Nevada and areas of the north coast. Areas of decreasing climatic suitability and increasing housing density were largely concentrated within the Central Valley. Our analyses suggest that the cumulative effects of future housing development and climate change will be large for many bird species, and that some species projected to expand their distributions with climate change may actually lose ground to development. This suggests that a key climate change adaptation strategy will be to minimize the impacts of housing development. To do this effectively, comprehensive policies to guide land use decisions are needed at the broader scales of climate change.

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Introduction

Climate change is projected to alter the distributions of many species. An array of species-distribution models (SDMs) is being used to identify species at risk from climate change (Midgley et al. 2002; Peterson et al. 2002; Thomas et al. 2004) as well as those whose ranges may expand (Guisan and Theurillat 2000). Where a species will be able to persist, however, is determined by habitat availability as well as climate (Warren et al. 2001; Hill et al. 2001; Reif et al. 2010). Changing land use is projected to increase rates of habitat loss in many parts of the world (Millennium Ecosystem Assessment 2005). Thus, the assumption that species can shift into any climatically suitable area may render projections based on climate alone incomplete. The vulnerability of species to environmental changes may consequently be underestimated (Travis 2003).

Although most SDM-based projections have focused only on climate-change, some recent efforts have incorporated the potential impacts of future land-use and landscape change on biodiversity and distributions (e.g., Barbet-Massin et al. 2012). At a global scale, these studies have found that habitat loss due to changes in land use may pose a greater immediate threat to biodiversity than climate change (Sala et al. 2000; Jetz et al. 2007). Because land-use planning, resource management, and conservation are carried out at local to regional scales, however, it is important to identify how climate, land use, and land cover interact to affect distributions at these finer scales (Warren et al. 2001; Forister et al. 2010). Finer-scale investigations permit a more detailed identification of species vulnerabilities to the combined impacts of land-use and climate change (Dirnböck et al. 2003; Bomhard et al. 2005; Pompe et al. 2008). In this context, examining land-conversion types beyond broad categories of habitat loss allows for a more detailed assessment of the effects on biodiversity (de Chazal and Rounsevell 2009).

In the United States, low-density housing development is the fastest growing form of land-use change (Theobald 2001; Hansen et al. 2005). Although urban development has often been identified as a primary threat to native species (Wilcove et al. 1998; Davies et al. 2006), many species may also be negatively affected by suburban and/or exurban development (Stralberg and Williams 2002; Pidgeon et al. 2007; Merenlender et al. 2009). Habitat quality can vary greatly within a given development density, and long-term studies suggest that development-

induced habitat fragmentation and degradation can lead to the gradual local extinction of many native species (Crooks et al. 2001). The increasing interface between housing and wildlife habitat may also be problematic for biodiversity conservation (Theobald et al. 1997; Hammer et al. 2007; Radeloff et al. 2010). Of course, birds respond differentially to different intensities of development in ways related to their life-history strategies (Johnston 2001; McKinney 2002; Blair 2004; Lepczyk et al. 2008), and many generalist species in particular may respond positively to housing development (Fraterrigo and Wiens 2005; Merenlender et al. 2009).

Bioclimatic niche differences among species may also result in a wide range of responses to climate change (Stralberg et al. 2009). Combined, the impact of these two factors will vary between species and across the landscape. Thus, it is useful to consider a first approximation of housing development (hereafter “development”) effects on native avifauna by estimating the area of spatial overlap between projected species distributions and projected future development. Accordingly, we used an SDM approach to assess potential changes in climatic suitability for a representative group of native California bird species, with climate projections tied to the same global population and economic growth assumptions as development projections. Using these SDMs, we quantified the spatial influence of projected land-use changes for development densities from urban to exurban and used species development-sensitivity scores to assess how development impacts may vary among species sensitivity groups.

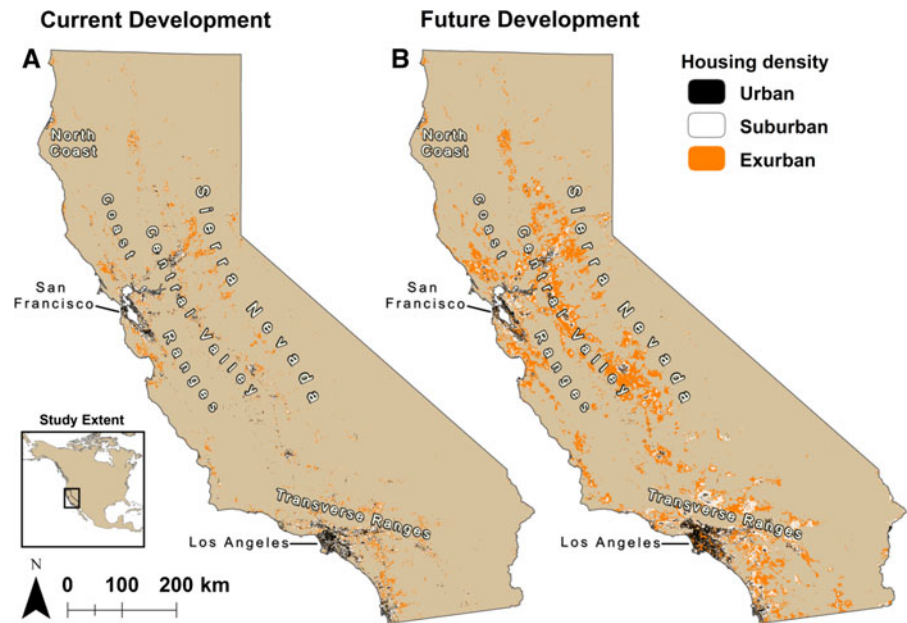
Our objectives were to (1) evaluate the relative potential impacts of climate change and development on bird species’ distributions in California; (2) compare the potential impacts of development across a range of densities; and (3) identify how all these impacts may vary regionally within the state. The results caution against considering the effects of either climate change or land-use change in isolation when projecting future changes in species’ distributions.

Methods

Study area

Our study area covers the entire state of California excluding islands (Fig. 1). We focused on California

Fig. 1 Current and future housing densities projected by the U.S. EPA (2009) under the IPCC SRES A2 scenario. See Table 1 for density definitions



because it supports high levels of biodiversity and endemism (Myers et al. 2000), it is likely to undergo rapid growth of human population (State of California 2007), and housing growth may dominate land-use change (Radeloff et al. 2005). Additionally, the wealth of bird data available within the state makes it ideal for developing SDMs.

Avian data sources

Bird-distribution models were based on presence/absence information for breeding species from point-count survey data from over 25,000 locations. We considered 64 focal species identified by California Partners in Flight as representative of six major vegetation communities: coniferous forest (17 species), oak-woodland (18), chaparral/scrub (11), riparian woodland (8), desert (7), and grassland (3) (Chase and Geupel 2005; Supplementary Material A). Data were obtained from several sources available through the California Avian Data Center (Ballard et al. 2008) including (1) PRBO Conservation Science (1993–2007), (2) USDA Forest Service Redwood Sciences Laboratory and Klamath Bird Observatory (1992–2006), (3) the North American Breeding Bird Survey (BBS) (1997–2006; Sauer et al. 2008), and (4) the California Department of Fish and Game. All data sets consisted of repeated surveys of all birds seen or

heard from a geo-referenced point location. Although metrics such as bird density and abundance could be obtained from these datasets, we used presence and absence information because it is most reliably standardized across surveys, especially given multiple data sources. We assumed that any species detected at any distance from a point was present at that location. All bird data were then aggregated to 800 m grid cells to match the spatial resolution of the climate data. Any species not detected at any of the points within a grid cell was considered absent. BBS transects consist of 50 points each spaced approximately 0.5 mile apart (approximately 805 m) along 24.5 mile (39.4 km) transects. We converted BBS routes to points by interpolating 50 evenly spaced points along each transect. Although this interpolation resulted in errors of spatial accuracy, our aggregation of the data onto 800 m cells reduced the effect.

To remove non-breeding records, data were filtered to include only records from April through July (i.e., the breeding season), with exceptions made for species that are known to breed in the desert areas of southern California, which were surveyed earlier in the year. To remove detections of non-breeding migrants, we omitted records that occurred outside of a species' known breeding range, as mapped by the California Wildlife Habitat Relationships System (Zeiner et al. 1988).

Current and future climate projections

Current climate data were based on 30 year (1971–2000) monthly climate normals interpolated at an 800 m grid resolution by the PRISM Group (Daly et al. 1994). We used monthly means for total precipitation and minimum and maximum temperature to derive a set of 19 biologically meaningful climate variables representing annual and seasonal variation as well as extremes. All variables are described and scripts to produce them are available at <http://www.worldclim.org/bioclim>. To remove the most highly correlated variables, we calculated Pearson correlation coefficients for each pair of climate variables (based on values at bird-survey locations) and identified any pair for which $r > 0.90$. We then removed the more complex variable of these pairs (defined as any variable that combined both temperature and precipitation, as the relationships between these variables may decouple in the future). This resulted in a total of eight candidate climate variables (Supplementary Material B).

Future climate was based on projections from a regional climate model (RCM), RegCM3 (Pal et al. 2007) run by the Climate Change and Impacts Laboratory (<http://ccil.ucsc.edu/~ccil/>) at a 30 km resolution, with emissions trajectory from the Intergovernmental Panel on Climate Change (IPCC) SRES A2 scenario, a high emissions scenario (IPCC 2007). To include and examine potential variability between global climate models (GCMs), we used output from two RCM runs based on boundary conditions from two GCMs: (1) the National Center for Atmospheric Research Community Climate System Model 3.0 (CCSM), run for 2038–2069; and (2) the Geophysical Fluid Dynamics Laboratory Climate Model 2.1 (GFDL), run for 2038–2070. Stralberg et al. (2009) provide more detail on climate data sources and variables used.

Current and projected housing development

We used current and future continuous housing-density grid surfaces developed by the Integrated Climate and Land-use Scenarios project (ICLUS; model details are provided in U.S. EPA 2009). Although other housing growth models are available for California (e.g., Johnston et al. 2008; Radloff et al. 2010), the ICLUS data set explicitly integrates parameters outlined by the IPCC A2 scenario, matching the climate-model scenario and

time frame used in our species models. Current housing density layers for ICLUS were based on the 2000 U.S. Census Bureau housing and population census block data. As a component of the ICLUS project, the allocation of a changing population to housing units was performed using the spatially explicit regional growth model (SERGoM; Theobald 2005), which uses the census-block data along with road and groundwater-well density, undevelopable lands (e.g., National parks, lakes), and population projections to create a spatially explicit grid of current and future development density. We used future housing densities averaged for 2060–2070. The IPCC A2 scenario is characterized by high fertility, high domestic migration, medium international migration, and increasing household size. Domestic migration is informed by a gravity model based on independent variables such as population size and distance. Current and future land-use grid surfaces represent housing densities modeled at a 1 ha resolution. To match the resolution of our climate grids, land-use data were resampled to an 800 m pixel resolution. Because we were interested in potential impacts across broad housing-density classes, we partitioned the continuous density grid into three classes: >12.4 units/ha (urban), 2.47–12.4 units/ha (suburban), and 0.247–2.47 units/ha (exurban), following Beardsley et al. (2009). Manipulation of environmental grid surfaces was conducted in ArcGIS 9.2 (ESRI 2006).

Models

For each bird species, we generated predicted current probabilities of occurrence in each 800 m grid cell based on mapped vegetation types and observed climate (1971–2000), as well as stream proximity, which was used as a proxy for riparian vegetation. The vegetation layer was based on vegetation models and types described in detail in Stralberg et al. (2009). Briefly, we used current vegetation mapped by the California Gap Analysis Project (Davis et al. 1998), aggregated to 12 general vegetation types, to model future vegetation based on current observed relationships between vegetation, climate, soil characteristics, solar radiation, and slope. Predictor variables for both bird and vegetation models are summarized in Supplementary Material B.

For the bird models, we implemented generalized additive models (Hastie and Tibshirani 1990) using the ‘gam’ package for R (R Development Core Team

2010) with a logit link function using smoothing splines with default target degrees of freedom (four) to ensure that the models were not over-fitted to the current dataset. We used a stepwise (forward and backward) AIC-based variable-selection approach to identify a predictive model for each bird species (Supplementary Material C). Future projections used the modeled future vegetation layer and future climate surfaces. Although stepwise model selection has been criticized for a potential bias in parameter estimates and its implications for hypothesis-testing (e.g., Whittingham et al. 2006), it was not our objective to identify the specific climate variables driving each species' distribution. Rather, we sought to build reasonable predictive models that could be used to evaluate the relative magnitudes of the effects of projected future climate and land-use change on multiple bird species. We used predicted probabilities of occurrence for all analyses of model outputs.

Model discrimination was evaluated using the area under the curve (AUC) of the receiver operating characteristics (ROC) plot (Fielding and Bell 1997) for 25 % of the data randomly withheld from the models (Supplementary Material A). Final models used in the analysis were run with no data withheld. Model reliability was evaluated using plots generated with the package “verification” in R and Brier scores (see details in Supplementary Material B).

Climate versus housing development analysis

To estimate the effects of climate change on species occurrence, we calculated the change in probability of occurrence between current and future SDMs for each species. Similarly, we estimated development impacts on future species distributions by calculating the change in probability of occurrence between future SDMs with current developed areas removed and future SDMs with future developed areas removed for each species and each of the three housing-density classes. This calculation provided the change in probability within future development areas while accounting for areas already developed. To express these changes in units of area, we multiplied the projected change in probability of occurrence by the area of each pixel (in km²) and then summed across all pixels to obtain a predicted area of change for each species.

To constrain our climate-impact calculations to suitable habitat, areas currently classified as urban or commercial were excluded from SDM outputs for the climate-change impact calculations. Because future commercial development was not modeled, current commercial areas were also excluded for development-impact calculations. We did not consider the effects of future agricultural development, for which statewide spatial projections are not readily available. Current agricultural areas were included in our models and area calculations and were assumed to remain unchanged into the future unless converted to housing development as projected by the ICLUS model.

Calculations of the areas affected by climate and land-use change were conducted by species as raster operations in R. For a given species, Csd is a grid representing current predicted area of occurrence based on climate, Fsd is the future projected area of occurrence based on changes in climate, Chd is the area of current housing development, and Fhd is the area of future housing development. Then, in set theory notation, where the set difference of F and C , denoted $F \setminus C$, is the set of all pixels of F that are not pixels of C :

Δ_C = Change in predicted area of occurrence due to climate = $(Fsd - Csd) \setminus Chd$.

Δ_D = Change in predicted area of occurrence due to development = $(Fsd \setminus Fhd) - (Fsd \setminus Chd)$.

Δ_O = Overall change in predicted area of occurrence = $\Delta_C + \Delta_D = (Fsd \setminus Fhd) - (Csd \setminus Chd)$.

To compare the overall effects of climate and development, we summed the total changes in predicted area of occurrence separately for climate-related increases, climate-related decreases, and land-use-related decreases for each housing-density class, averaged between GCMs and summed across all species. To examine the variability of our results among species and GCMs, we partitioned the results into the six Partners in Flight focal-species groups for each GCM and for the average across GCMs. Finally, we classified species according to the impact of climate and the relative impact of total development (averaged across GCMs).

Development-sensitivity scores

Although our SDMs provided explicit information on probabilities of species occurrence, our analysis of development only provided information on how much

of a species' range may be impacted by each development density. Thus we interpreted results in the context of development-sensitivity scores based on life-history features as described in Hansen and Urban (1992), supplemented by information from Poole (2009). Life-history data included nesting characteristics (nest type, nest height), reproductive effort, and migratory behavior. Development-sensitivity scores had a possible range of 5–15, with higher numbers indicating greater sensitivity to development. Species with higher reproductive output, smaller area requirements, more general nesting habitat, and short-distance to no migration (i.e., generalist species) were considered less sensitive to development and received lower sensitivity scores. Thus, these species may be better able to maintain viable populations within developed areas while species with higher scores were considered less able to do so.

Geographic variability

To illustrate geographic patterns in climate and development impacts, we mapped current and future distributions overlaid with housing development for the oak-woodland and coniferous forest bird groups, two groups that captured the variation in responses to

Table 1 Housing density class definitions and total area (rounded to nearest km²) of each class in California for 2000 and 2060–2070 as projected by the U.S. EPA (2009) under the IPCC SRES A2 scenario

Housing density type	Density (units/ha)	Area in 2000 (km ²)	Area in 2070 (km ²)
Urban	>12.4	25,361	47,325
Suburban	2.47–12.4	66,001	150,750
Exurban	0.247–2.47	109,332	321,009

Table 2 Mean \pm SD values for selected climate variables summarized for the state of California for the current period and two future climate model projections (NCAR 2038–2069; GFDL 2038–2070) based on the IPCC A2 scenario

Climate variable	Current	NCAR CCSM3.0	GFDL CM2.1
Annual mean temperature (°C)	14.2 \pm 4.6	15.9 \pm 4.6	16.4 \pm 4.6
Temperature seasonality ^a (°C)	6.30 \pm 12.4	6.83 \pm 13.5	7.01 \pm 1.33
Annual precipitation (mm)	613.0 \pm 535.8	418.4 \pm 378.2	562.5 \pm 496.0
Precipitation seasonality ^b	77.5 \pm 16.4	84.2 \pm 14.6	90.5 \pm 17.8

^a Standard deviation of monthly mean temperature

^b Coefficient of variation of monthly precipitation

climate. To identify regions that may be particularly vulnerable to changes in both climate and development, we combined and mapped the changes in species probability of occurrence and development density between current and future periods. Change in combined species probability of occurrence was calculated by taking the difference between the future and current sums of all future species' probabilities of occurrence (averaged across GCMs). Change in development density was calculated as the difference between future and current housing density (units/ha). The 800 m grids of change in combined species probability of occurrence then were overlaid with the changes in housing density to highlight regions where both factors were projected to have large impacts.

Results

For the IPCC A2 scenario we examined, future development in California is projected to be concentrated in the Central Valley, the foothills of the Sierra Nevada, on both sides of the transverse ranges in southern California, and the San Francisco Bay area (Fig. 1). Urban and suburban areas are projected to nearly double by 2070, while exurban development is projected to triple (Table 1).

Both climate models we examined project increased temperatures and reduced annual precipitation (Table 2). In comparison with the CCSM climate projection, the GFDL projection is on average hotter, with greater precipitation and more seasonality.

Model performance for current predictions of individual species' distributions was good to excellent for all species based on ROC AUC scores (0.91 ± 0.055 SD; Swets 1988) and Brier scores (Supplementary Material A).

Relative impacts of climate and development

Averaged across GCMs, species responding positively to climate change were projected to gain 253,890 km² and species responding negatively were projected to lose 335,640 km². Development resulted in a potential loss of approximately 164,268 km², averaged across GCMs.

The oak-woodland and chaparral/scrub-associated groups were the only groups projected to have a net increase in distribution with climate change (Fig. 2). The impact of development was apparent for all but the coniferous forest group, where it accounted for less than 2 % of the total (i.e., both climate and development) potential loss in predicted area of occurrence. Development-driven losses were greatest in both area and percentage (compared to total losses) within the oak-woodland group, followed by the chaparral/scrub group. The oak-woodland group lost a total of 95,000 km² to development, equal to 80 % of their total area loss. The chaparral/scrub group lost a total of 27,174 km² to development, equal to 49 % of their total area loss. The development-driven decreases for desert, grassland, and riparian-woodland bird groups

represented 34, 18, and 18 %, respectively, of their total decreases.

Of the 64 species we examined, 24 were projected to increase their predicted area of occurrence with climate change. Of these increases, five were completely counteracted by development-driven losses and an additional five had development-driven losses greater than 50 % of the climate-driven gains (Table 3). Of the 40 species with projected decreases due to climate change, four had decreases due to development greater than those due to climate, and an additional four had development-related decreases greater than 50 % of climate-driven decreases.

Species with high development-sensitivity scores (42 of 64 with scores ≥10) followed similar patterns, but a greater proportion had projected decreases in area of occurrence due to climate change (Table 3). All eight species that were projected to have both large development-driven decreases (greater than 50 % of climate impacts) and negative responses to climate had high development-sensitivity scores. Large development-driven decreases were projected for an additional ten species, four of which had high development-sensitivity scores. Development-

Fig. 2 Total change in area of occurrence (km²) between current and future climate and housing development scenarios for three development density categories (urban, suburban, exurban). For each of the six focal-species groups, values are presented for each individual GCM and for the mean across GCMs

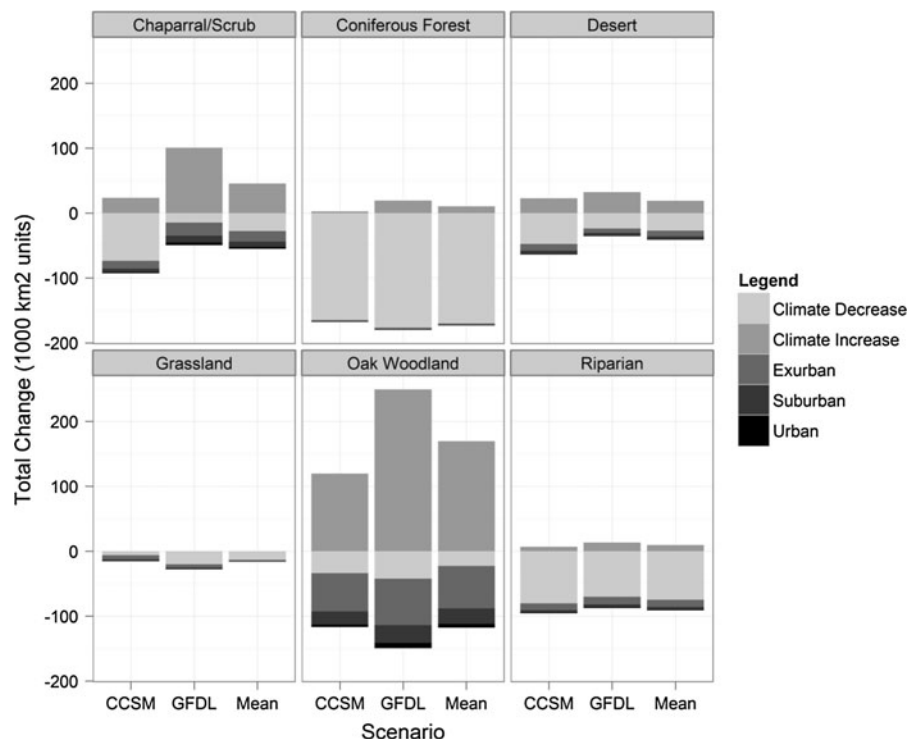


Table 3 Species ordered by impact of development and climate, averaged across climate models where (1) species are projected to increase or (2) decrease due to climate and development has (A) a greater impact than climate, (B) an impact equal to or greater than 50 % of climate impact, (C) an impact equal to or greater than 25 % of climate impact, or (D) has an impact that is less than 25 % of climate impact. High development-sensitivity scores are defined as 10–15 and low sensitivity scores are defined as <10. Species scientific names are provided in Supplementary Material A

A	B	C	D
Development \geq climate	Development ≥ 50 % climate	Development ≥ 25 % climate	Development <25 % climate
(1) Climate increase			
Blue Grosbeak ^{1,R}	Wren ^{1,S}	Ash-throated Flycatcher ^{1,O}	Black-throated Gray Warbler ^{1,C}
Turkey Vulture ^{1,S}	Common Raven ^{1,D}	Common Yellowthroat ^{1,R}	Rufous-crowned Sparrow ^{1,S}
Western Scrub-jay ^S	California Towhee ^O	California Thrasher ^{1,O}	Sage Sparrow ^{1,S}
Bewick's Wren ^O	Nuttall's Woodpecker ^O	Purple Finch ^{1,C}	Blue-gray Gnatcatcher ^{1,O}
White-breasted Nuthatch ^O	Hutton's Vireo ^O	Acorn Woodpecker ^O	Scott's Oriole ^{1,D}
		Oak Titmouse ^O	Greater Roadrunner ^S
			Ladder-backed Woodpecker ^P
(2) Climate decrease			
Western Meadowlark ^{1,G}	Black-headed Grosbeak ^{1,R}	Allen's Hummingbird ^{1,S}	Fox Sparrow ^{1,C}
Spotted Towhee ^{1,S}	Mountain Quail ^{1,S}	Black-tailed Gnatcatcher ^{1,D}	MacGillivray's Warbler ^{1,C}
California Quail ^{1,O}	Red-shouldered Hawk ^{1,O}	Cactus Wren ^S	Swainson's Thrush ^{1,R}
Phainopepla ^{1,D}	Lark Sparrow ^{1,O}		Varied Thrush ^{1,C}
			White-crowned Sparrow ^{1,S}
			Wilson's Warbler ^{1,R}
			Costa's Hummingbird ^{1,S}
			Warbling Vireo ^{1,R}
			Savannah Sparrow ^{1,G}
			Black-throated Sparrow ^{1,D}
			Yellow-rumped Warbler ^{1,C}
			Western Tanager ^{1,C}
			Song Sparrow ^{1,R}
			Band-tailed Pigeon ^{1,O}
			White-tailed Kite ^{1,G}
			Verdin ^{1,D}
			Gray Flycatcher ^{1,C}
			Chipping Sparrow ^{1,C}
			Steller's Jay ^{1,C}
			Brown Creeper ^C
			Tree Swallow ^R
			Cassin's Finch ^C
			Clark's Nutcracker ^C
			Dark-eyed Junco ^C
			Golden-crowned Kinglet ^C
			Pileated Woodpecker ^C
			Wood Duck ^O
			Yellow-billed Magpie ^O
			Red-breasted Nuthatch ^C

/ high development-sensitivity score, C conifer, G grassland, O oak, R riparian, S scrub

sensitivity scores for the study species ranged from 6 to 13 (Supplementary Material A).

Comparative impacts across housing densities

Most of the spatial impact of future development on predicted area of occurrence was associated with suburban and exurban growth (27 and 66 % of overall development-driven area losses, respectively). Averaged across all species, suburban and exurban development accounted for 9 and 22 % of total area losses, respectively. For the oak-woodland group, exurban development accounted for over half (55 %) of the total decrease in predicted area of occurrence. For the chaparral/scrub and desert group, exurban development accounted for 29 and 21 % of the total decrease in predicted area of occurrence, respectively.

Regional patterns

Oak-woodland-associated bird species were generally projected to increase due to climate change, primarily by shifting distributions toward the north and central coast and to greater elevations along the foothills of the Sierra Nevada. This is where exurban growth is projected to increase greatly (Fig. 3a–c). Coniferous forest species were projected to face minimal impacts from development, in part because their current distributions were projected to shrink away from developing areas along the lower elevations of the Sierra Nevada (Fig. 3d–f). Areas of climate-projected decreases in overall species probability of occurrence that coincided with projected increases in housing density were prevalent across much of the Central Valley and portions of the foothills of the Sierra Nevada, as well as around San Francisco Bay and along the northern side of the Transverse Ranges (Fig. 4).

Discussion

Our analysis of the combined effects of future climate change and housing development on bird distributions shows that the potential impacts of development can be as great as or greater than those from climate change for many species. Even if climate change leads to an increase in the area of a species' occurrence, the gains could be partially or completely undermined by

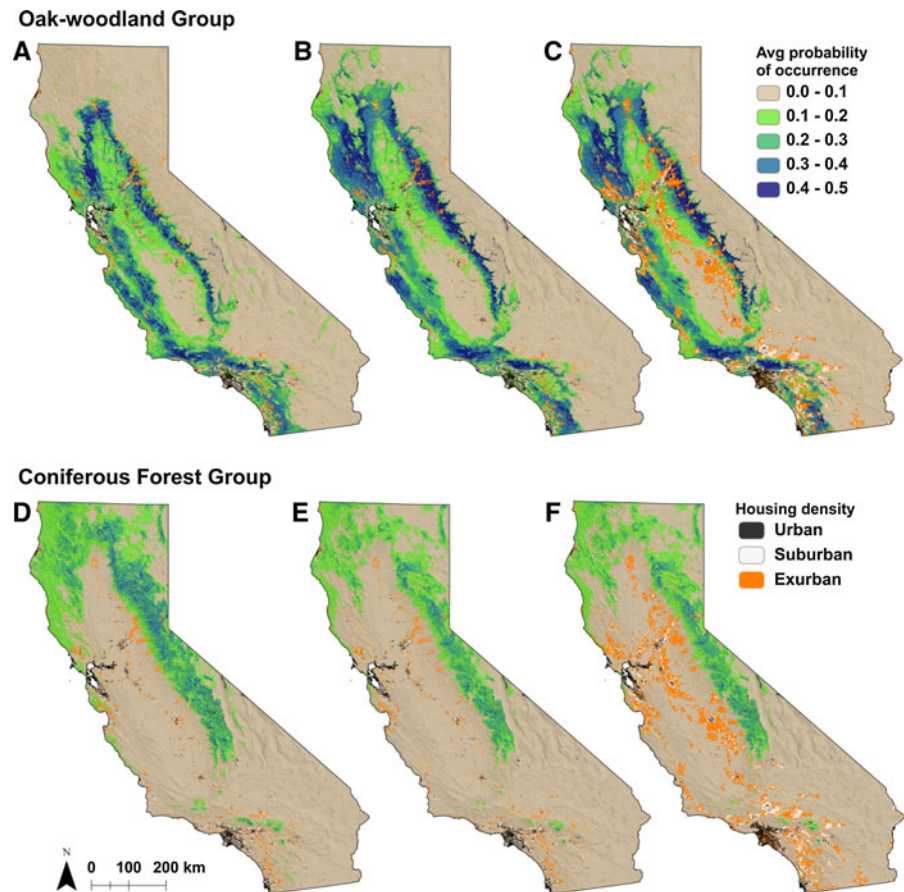
development impacts, as shown by the oak-woodland-associated group of species. Our results align with those of other studies (Bomhard et al. 2005; Jetz et al. 2007; de Chazal and Rounsevell 2009) that highlight the need for conservationists, resource managers, planners, and policy-makers to consider the effects of land-use change as part of any climate-change adaptation strategy.

Our analysis included a range of development densities that may impact wildlife in a variety of ways, including habitat loss, fragmentation, and degradation (Theobald et al. 1997; Marzluff et al. 2001; Hansen et al. 2005; Pidgeon et al. 2007). Due to human population and economic growth patterns, future suburban and exurban development in California may have particularly large impacts on vegetation communities and the birds that depend on them. In the scenario we examined, suburban housing is projected to grow nearly four times as fast, and exurban housing nearly ten times as fast, as high-density urban housing. Although the habitat quality and avian responses associated with low-density development may vary greatly, the majority of native species that we evaluated may be considered development-sensitive to some degree and may experience negative consequences from housing development, especially over the long term.

Development pressures and climate change are widely recognized as stressors to wildlife, but they tend to be considered in isolation, reducing the effectiveness of conservation or land-management actions (Sala et al. 2000; Pyke 2004). Our results indicate that both threats may vary in different combinations across the landscape. Such information can provide useful guidance for informing and prioritizing landscape planning. For example, our models project that the Central Valley will experience the largest climate-induced decreases in overall species probability of occurrence along with the highest levels of development. Here, landscape planning that reduces or mitigates the threat of development, combined with connectivity-focused habitat protection and restoration efforts (Spencer et al. 2010), may be especially useful.

In contrast, some lower-elevations in the Sierra Nevada may experience increases in probability of occurrence for several species in association with climate change, but may also face potentially large development impacts. Here, prioritizing areas for

Fig. 3 Current predicted areas of occurrence averaged for **a** oak-woodland and **d** coniferous forest associated species overlaid with current housing development densities. Future projected areas of occurrence for **b** oak-woodland and **e** coniferous forest associated species overlaid with current development densities. Future projected areas of occurrence for **c** oak-woodland and **f** coniferous forest associated species overlaid with future development densities. See Fig. 1 for geographic area references



long-term conservation easements and ecological reserves along with reducing the impacts of development may help ensure the persistence of future species-rich areas that would otherwise be lost. Our models also show that higher elevations within the Sierra Nevada as well as areas of the north coast may support increases in overall species probability of occurrence with relatively little direct impact from development. However, many of the coniferous forest-associated species projected to move into these regions are also development-sensitive, indicating the importance of holding development threats at bay.

The relative impacts of climate and development are likely to differ markedly among species. Within our scenarios, coniferous-forest-associated species would benefit from a focus on managing climate-related impacts, whereas an aggressive effort to manage housing development could be critical to the viability of chaparral/scrub-associated species in California. The same may be true for oak-woodland-

associated species, despite projected increases in species distributions due to climate change.

Limitations and assumptions

Although the climate and development projections we used are part of a closely examined and well-documented future storyline (IPCC 2007), this is only one scenario of several that could be examined to guide planning decisions. All models are plagued by uncertainty, and this is particularly true of attempts to model future climates (Wiens et al. 2009). The two climate models we used agree in their projections that the future will be warmer and drier, but differences in the projected magnitudes of change result in variable projections for desert and chaparral/scrub-associated bird species in particular. In addition, the uncertainty of model predictions may increase if temperatures increase beyond the range currently found within an area. Because our models were informed by current

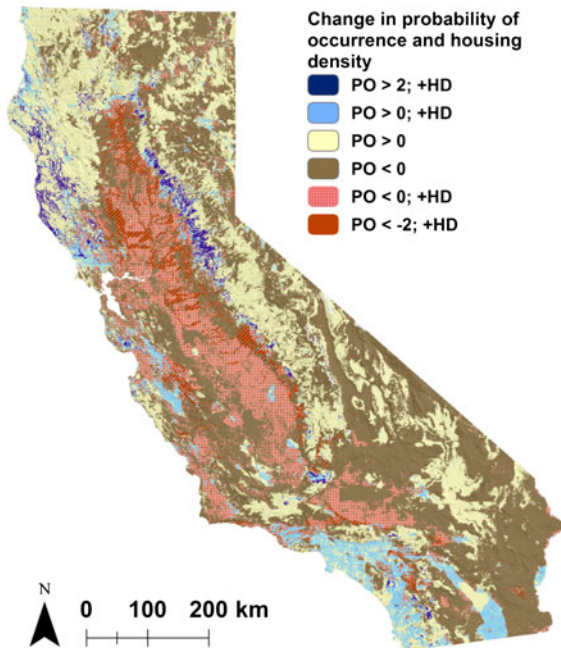


Fig. 4 Changes in overall species probability of occurrence due to climate change (PO) coinciding with increases in housing density (HD) calculated as the difference between current and future time periods. Shades of blue indicate increases in PO coinciding with increasing HD. Shades of red indicate decreases in PO coinciding with increases in HD. Changes in probability of occurrence were calculated as the total change across all species

climate conditions, future climate change may bring conditions that do not presently exist in the area (no-analog climates), potentially forcing the models to project beyond the calibration data. This may result in under- or over-prediction within no-analog areas (Fitzpatrick and Hargrove 2009), which may comprise some 6 % of the state (Wiens et al. 2011). Most of these projected no-analog climate areas occur in the southeastern desert portions of the state, which may explain the relatively high variability in projections for desert-associated species. These regions tend to have low projected development, however, so the uncertainty is not likely to affect our results.

Our models did not incorporate the possibility of imperfect detection (*sensu* Mackenzie et al. 2003) from the point count surveys used to train the models. If the surveys failed to detect a species within an otherwise suitable environmental space, our results could under- or over-estimate the relative effects of development on the species, depending on how that environmental space was impacted by housing

development. However, over 70 % of all surveyed cells had at least five visits. Thus, detectability would have to be quite low for a species to go undetected in a large majority of our cells. Moreover, we only considered data collected during the breeding season, when bird species are most active and singing to attract mates, and none of our focal species could be considered secretive. Thus, any bias introduced at the cell level is likely minimal, especially when considering the statewide scale of our analysis.

Although not accounted for in our projections, exurban development may still provide useful habitat for many species, and even increase the numbers of some. The scarcity of point-count surveys collected at the high end of the housing density gradient prevented us from directly modeling the effects of development on individual bird species distributions in California (but see Lepczyk et al. 2008). This remains an important goal for future modeling efforts. However, while some species may actually benefit from anthropogenically modified habitat (Fraterrigo and Wiens 2005; Chace and Walsh 2006), most do not (Lepczyk et al. 2008). Despite the frequently detected pattern of higher bird species richness at intermediate levels of development intensity (Blair et al. 1996; Desrochers et al. 2011), anthropogenic activities have also resulted in the homogenization of bird communities over time (La Sorte and McKinney 2007), a trend that may be expected to continue in the future.

Our projections of the effects of land-use change are conservative in several ways. We did not consider the influence of developed areas as barriers to climate-induced distribution shifts (Harris and Reed 2002), nor did we consider the impacts of other infrastructure that accompanies and is closely tied to housing, such as roads, utilities, or commercial buildings (Burchell et al. 2002). In addition, agriculture has a large impact on habitat availability and suitability, but we were unable to consider this aspect of future land-use change because high-resolution future projections for agricultural land use are not available for California. Although options for further increases in agricultural area may be limited, the types of agriculture that now exist may change. Neither did we address the impact that past development has already had on species diversity and distributions. Finally, our analysis did not account for the possible synergies that may occur between these two drivers of landscape and biodiversity change (Pyke 2004; Brook et al. 2008).

Conclusions

Many species will face myriad challenges brought about by climate change. Because current levels of atmospheric greenhouse gases have locked in a climate-change pathway that will persist for decades (Sokolov et al. 2009), management strategies must be geared toward climate-induced stresses that have yet to emerge. Reducing the exposure of species to current stressors such as development and habitat degradation can increase their resiliency and reduce their vulnerability in the face of climate change (Chapin et al. 2010). Focusing on landscape-scale actions—the creation of corridors and buffers around currently protected areas, the designation of new protected areas, habitat restoration efforts, and regional landscape planning—will be increasingly important in dealing with the combined impacts of development and climate change (Heller and Zavaleta 2009). Because exurban development consumes roughly an order of magnitude more land per unit dwelling than urban development, these strategies align with the benefits of fostering compact development patterns or “smart” urban growth (Danielsen et al. 1999).

Landscape planning and conservation are caught between a rock (climate change) and a hard place (development). Developing and implementing effective strategies for conservation and landscape management in the future requires land-use planning that incorporates the potential consequences of climate change, and climate-change projections that incorporate the potential effects of changing land uses and development. Efforts to bring together resource conservation partners at the landscape scale, such as the Landscape Conservation Cooperatives (U.S. Department of the Interior 2009), will benefit from integrating and working closely with land-use planners. There is little comprehensive policy to guide land-use and development decisions at the broader scales of climate-change projections. Analyses such as those we have presented here can help by identifying those species, groups of species, habitats, and places that may be especially vulnerable to both climate change and development.

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