

# Niches, models, and climate change: Assessing the assumptions and uncertainties

John A. Wiens<sup>a,1</sup>, Diana Stralberg<sup>a</sup>, Dennis Jongsomjit<sup>a</sup>, Christine A. Howell<sup>a</sup>, and Mark A. Snyder<sup>b</sup>

<sup>a</sup>PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954; and <sup>b</sup>Climate Change and Impacts Laboratory, Department of Earth and Planetary Sciences, University of California, 1156 High Street, Santa Cruz, CA 95064

Edited by Elizabeth A. Hadly, Stanford University, Stanford, CA, and accepted by the Editorial Board August 28, 2009 (received for review April 3, 2009)

As the rate and magnitude of climate change accelerate, understanding the consequences becomes increasingly important. Species distribution models (SDMs) based on current ecological niche constraints are used to project future species distributions. These models contain assumptions that add to the uncertainty in model projections stemming from the structure of the models, the algorithms used to translate niche associations into distributional probabilities, the quality and quantity of data, and mismatches between the scales of modeling and data. We illustrate the application of SDMs using two climate models and two distributional algorithms, together with information on distributional shifts in vegetation types, to project fine-scale future distributions of 60 California landbird species. Most species are projected to decrease in distribution by 2070. Changes in total species richness vary over the state, with large losses of species in some “hotspots” of vulnerability. Differences in distributional shifts among species will change species co-occurrences, creating spatial variation in similarities between current and future assemblages. We use these analyses to consider how assumptions can be addressed and uncertainties reduced. SDMs can provide a useful way to incorporate future conditions into conservation and management practices and decisions, but the uncertainties of model projections must be balanced with the risks of taking the wrong actions or the costs of inaction. Doing this will require that the sources and magnitudes of uncertainty are documented, and that conservationists and resource managers be willing to act despite the uncertainties. The alternative, of ignoring the future, is not an option.

birds | California | ecological niche | species distribution models | conservation

The world is changing rapidly, because of the cascading and intertwined effects of human population growth, widespread poverty, economic globalization, land-use change, and, looming over it all, climate change. These changes are having profound effects on biological diversity, effects that will only become more dramatic and dire as the pace of environmental change quickens. The challenges to conservation and environmental management are immense.

Traditionally, conservation has focused on protecting individual species and their habitats. This focus derives from more than a century of work describing the relationships between organisms and features of the environment. Virtually all of this work has been shaped by thinking about ecological niches. Niche concepts and theory, in the form of “ecological niche models” or “bioclimatic envelope models” (1, 2), have become central in efforts to understand how future climate change may have an impact on species and their habitats. In this paper, after providing a brief perspective on “ecological niches,” we describe how niche thinking and modeling have been used to project changes in the distributions of species and consider several assumptions and uncertainties. We illustrate the approach with examples from our work on California birds and conclude by assessing the usefulness of niche-based models for projecting climate-change impacts on biodiversity and the implications for conservation and management.

## A Brief Perspective on Niches

The foundations for thinking about ecological niches were laid by Joseph Grinnell and Charles Elton in the 1910s and 1920s. Grinnell (3) thought of the niche as a subdivision of the habitat containing the environmental conditions that enable individuals of a species to survive and reproduce. These conditions determine where a species will occur—its distribution and abundance. Elton’s (4) notion of niches, published a decade after Grinnell’s, emphasized the functional role of a species in a community, especially its position in food webs. The focus was less on where a species could occur and more on its interactions with other species in a community. Elton’s view was the foundation for the later applications and elaborations of the niche concept by Lack (5) and, especially, Hutchinson (6) and MacArthur (7). Niches were defined by dimensions in resource utilization space rather than the environmental dimensions that characterized Grinnell’s niches. As niche theory developed it became ever more closely associated with interspecific competition, to the extent that during much of the 1960s and 1970s “niche” and “competition” were virtually interchangeable terms (8, 9). When simplistic competition theory was challenged in the late 1970s and early 1980s (10, 11), niche theory also fell into the background, only to be resurrected as its potential relevance to modeling how species might respond to environmental change has become apparent.

The enduring insight from Hutchinson’s work is in the distinction between the *fundamental* and *realized* niche. Simply put, Hutchinson regarded the fundamental niche as the set of resources—physical and biological—that a species could use that would enable it to exist indefinitely. Thus, the fundamental niche is determined by intrinsic properties of a species—how it responds to the environment—rather than by extrinsic properties of the environment independent of the species. The realized niche is the subset of the fundamental niche to which a species is constrained by interactions with other species (competition, predation) with which its fundamental niche overlaps.

## The Use of Niche Thinking in Modeling Species’ Distributions in Response to Climate Change

Species can respond to climate change by shifting distribution to follow changing environments, by adapting to changing conditions in place, or, if unable to do either, by remaining in isolated

---

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, “Biogeography, Changing Climates and Niche Evolution,” held December 12–13, 2008, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and audio files of most presentations are available on the NAS web site at [www.nasonline.org/Sackler.Biogeography](http://www.nasonline.org/Sackler.Biogeography).

Author contributions: J.A.W., D.S., and D.J. designed research; D.S., D.J., C.A.H., and M.A.S. performed research; M.A.S. contributed new reagents/analytic tools; J.A.W., D.S., D.J., and C.A.H. analyzed data; and J.A.W., D.S., and D.J. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. E.A.H. is a guest editor invited by the Editorial Board.

<sup>1</sup>To whom correspondence should be addressed. E-mail: [jwiens@prbo.org](mailto:jwiens@prbo.org).

This article contains supporting information online at [www.pnas.org/cgi/content/full/0901639106/DCSupplemental](http://www.pnas.org/cgi/content/full/0901639106/DCSupplemental).

pockets of unchanged environment (“refugia”) or, more likely, becoming extinct (12). Although some attention has been given to the last three options (e.g., refs. 13–16), using “species distribution models” (SDMs) to project how the distributions of species may change under different scenarios of climate change has become especially popular (2, 13–15). Ecological niche models are the cornerstones of such distributional modeling. Such models use information on the environmental features that define the current ecological niche of a species in association with the future distributions of those features derived from climate-change models to project where the species’ niche requirements may be satisfied in the future.

Ecological niche models generally use one of two approaches, roughly corresponding to whether they adopt the fundamental or the realized niche as the frame of reference (2, 16, 17). The first approach is mechanistic, using information on the intrinsic properties of species that determine their sensitivity to physical features of the environment—their physiology, life-history, behavioral or genetic plasticity—to map current or future locations that fall within the tolerance limits of a species (e.g., refs. 18 and 19). The second approach is correlative: environmental variables characterizing places where a species does (or does not) occur are used to develop correlative models that can then be extrapolated to project future occurrences in places where the correlated environmental features are projected to be present. The emphasis is on extrinsic factors determining the distribution of a species—where it is, rather than where it could be. In recent years, the majority of niche modeling has been correlative, particularly when more than one species is involved (but see ref. 20). For that reason, and because the necessary mechanistic information is lacking for many of the species we consider, correlative models are our focus in this paper.

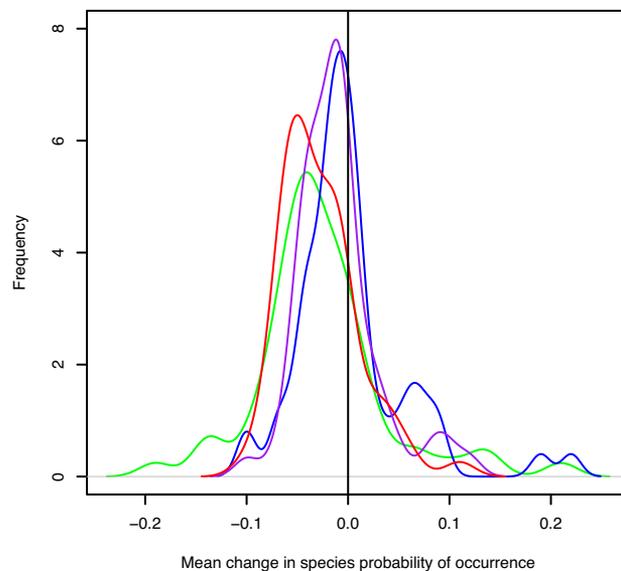
Despite the recent popularity of SDMs to project the potential consequences of climate change, enthusiasm for their use is not ubiquitous (21, 22). Like any models, SDMs rely on underlying assumptions and incorporate uncertainties (23). Understanding these assumptions and uncertainties is essential if the results of SDMs are to be used to inform conservation and management.

### Assumptions

Niche-based species-distribution models can produce high-resolution maps showing how the probabilities of species occurrences are likely to shift with climate change (e.g., Figs. 1–5 below). In topographically and environmentally diverse regions, these maps contain a wealth of beguiling detail and may portend a future quite different from the present. But how credible are the projections? Should the modeling results be used to guide land acquisitions for conservation, management of wildlife refuges, or other conservation or management activities, or are they only illusions of possible futures, interesting but not to be trusted for making decisions?

The answer, of course, lies somewhere between these extremes. To see where (and why), we must evaluate the assumptions underlying the approach.

**Correlations.** Correlative niche models are based on analyses that relate the occurrence of a species in places to features of those places. Using such models to project future distributions assumes that the variables included in the models do in fact reflect the niche requirements of a species. One can never measure all of the factors that determine a species’ niche, and the possibility that unmeasured niche dimensions may account for the observed distribution has plagued niche analyses for decades and generated considerable debate (8). Even “good” models may fail to provide accurate projections when extended to other places or times (24).



**Fig. 1.** Frequency distribution of species showing projected future change in mean probability of occurrence across all California 800-m pixels based on two distribution model algorithms (GAM and Maxent) and two climate models (GFDL CM2.1, Scenario A2, 2038–2070; and NCAR CCSM 3.0, Scenario A2, 2038–2069): blue, GFDL/GAM; purple, CCSM/GAM; green, GFDL/Maxent; red, CCSM/Maxent.

**Equilibrium and Habitat Saturation.** Using current environmental correlates of a species’ distribution to project its future occurrence also assumes that the current distribution is in equilibrium—suitable habitat is fully occupied or “saturated” (17, 25). Suitable places may be unoccupied, however, if recent disturbances have eradicated a species from an area [as visualized in metapopulation theory (26)], if a species is expanding into areas that have only recently become available, or if regional population density is inadequate to support colonization of suitable areas. On the other hand, time lags associated with longevity of individuals established under previous conditions [“legacy” effects in plant distributions (27)] or with breeding-area philopatry in birds may result in the occurrence of individuals in areas that no longer fall within their environmental niche space. Thus, ecological niche models may be prone to both omission errors (leaving out of the niche space information from places that could be occupied) and commission errors (including in the niche space places that cannot sustain the species) (28).

**Dispersal and Landscapes.** The assumption that locations within the environmental niche space of a species will be occupied requires that individuals will be able to disperse to suitable locations (16, 28). If environmental conditions shift more rapidly than individuals can disperse, however, the species may be relegated to persisting only in isolated habitat refugia that meet their niche requirements (25). The prospect that many species may not be able to keep up with the speed of movement of suitable environments under future climate change has fostered discussions of “assisted migration” as a conservation strategy (29).

The ability of individuals to disperse to suitable places is not solely a function of their inherent dispersal capacity. In many cases the landscape through which species must move to reach suitable places has been increasingly fragmented by human actions. This fragmentation breaks habitat connectivity, imposes barriers to dispersal, and creates a landscape mosaic of suitable, less suitable, and unsuitable habitat patches. The effects of landscape structure and connectivity on the future distributions

of species may become increasingly important as land-use change accelerates in many parts of the world. Indeed, some scientists have argued that the effects of land-use change on species distributions and species loss over the near future may exceed those of climate change (30–32).

**Biotic Interactions.** Most niche models implicitly assume that biotic communities are Gleasonian (33), each species responding independently to the environmental factors that determine its niche space, and thus its habitat occupancy and distribution. Thus, species interactions are generally not included in niche models (ref. 34, but see refs. 35 and 36), even though the effects of biotic interactions may sometimes supersede those of climate (37).

It is not hard to see why. Many species may co-occur in an area, creating the setting for a bewildering array of interactions with cascading direct and indirect effects. Documenting these interactions, even for a subset of species, is an overwhelming challenge, especially as the nature of the interactions and their effects on any one species may change from place to place (or time to time) as other species enter or leave an assemblage or their abundances change.

**Adaptation and Evolution.** Ecological niche models also assume niche conservatism (38), the notion that the niche envelope is a fixed and immutable characteristic of a species, unchanging over space and time. This assumption justifies using correlative niche models for a species from some locations to extrapolate its distribution to other locations that have not been surveyed. We know, of course, that local populations may be differentially adapted to local conditions (39). The assumption that the niche space of a species is stable over time is more germane to the use of SDMs to project responses to climate change. It is often argued that the rate of current and future environmental change exceeds the capacity of most plant and animal species to adjust evolutionarily (40). This may be true for long-lived species with limited dispersal, but there is mounting evidence that some short-generation species are capable of rapid evolutionary change (41). Rapid behavioral adjustments to changing environmental conditions may also be commonplace. The observation that some bird species are advancing the timing of spring migration or breeding activity in association with warmer temperatures (42) indicates a capacity to adjust to changing conditions within localities without shifting distributions. It is not obvious, however, that such behavioral adjustments represent viable adaptations to climate change, especially if, for example, the breeding phenology of the birds no longer matches the flushes of prey abundance required to feed offspring.

### Uncertainties

The future is by definition uncertain. Using models to project probable futures based on current information and understanding entails additional uncertainties. Some of these uncertainties are due to the assumptions underlying a modeling approach; to the extent that these assumptions are violated, uncertainty in the model projections is increased. But there are other sources of uncertainty as well (23, 43, 44).

**Climate Model Uncertainties.** Projections of shifts in species' distributions with changes in climate are derived by coupling niche models with projections based on general circulation models (GCMs) that describe potential future conditions at a coarse scale of resolution (typically 156–313 km). Because different GCMs rely on different parameters and incorporate different functions to portray the dynamics of atmospheric circulation, ocean effects, or feedbacks between the land surface and the atmosphere, they may project different consequences for the same level of greenhouse gas emissions. Projections for California derived by using the National Center for Atmospheric

Research (NCAR) PCM model with the A1fi emissions scenario (45), for example, suggest a temperature rise of 3.8 °C by the end of the century from the 1990–1999 baseline, whereas the Hadley CM3 model projects a temperature rise of 5.8 °C for the same emissions scenario (46).

The resolution of climate-model projections is increased by downscaling from GCMs to a regional or local scale. Statistical downscaling involves interpolations from empirical relationships among variables by using weather-station or GCM data, taking into account topography and local climate anomalies (47). Dynamical downscaling uses regional climate models (RCMs) that are nested within GCMs to simulate climate patterns at a finer scale than GCMs (e.g., 10–50 km) and that include a more detailed representation of land cover (48–50). Although statistical downscaling is computationally less demanding than dynamical downscaling, it is more dependent on the availability of adequate weather data and assumes that past relationships between local weather and regional climate will hold into the future. In contrast, dynamical downscaling can simulate nonlinear climate processes that are likely to change in the future. Although both approaches aim to incorporate the effects of topography, land cover, and climate anomalies, they are nonetheless constrained by the coarse-scale output of the GCMs that drive them (51).

**Distribution Model Algorithm Uncertainties.** Several algorithms have been developed to model the distributions of species based on species occurrence data. More traditional statistical methods such as generalized linear models (GLMs) or generalized additive models (GAMs; ref. 52) require species absence (or pseudo-absence) as well as presence information, as do artificial neural networks (53) and genetic algorithms (GARP; ref. 54). Other algorithms have been developed for presence-only data, including simple envelope models such as DOMAIN (55) and BIOCLIM (56), as well as more sophisticated machine-learning algorithms such as Maxent (57). Comparative studies have found a range of performance across algorithms and no single method emerges as “best” (58–60). For example, GARP generally has high model sensitivity but also a high rate of false positives (59, 60), which may result in predictions that are spatially over-inclusive, whereas DOMAIN (20) and tree-based approaches (59) tend to have high model specificity but also a high false-negative rate, therefore tending to underpredict. Model validations on independent datasets have suggested that some of the newer machine-learning (e.g., Maxent) and tree-based (e.g., boosted regression trees) algorithms have the best overall performance, in terms of both sensitivity and specificity (58–61).

**Data Uncertainties.** Any modeling exercise is sensitive to the quality and quantity of the underlying data, and SDMs are no exception. For climate data, the spatial and temporal resolution (e.g., spatial distribution and duration of weather records) affect the downscaling of GCMs, and differences in the broad climatic variables used to drive GCMs can result in different projections, increasing model uncertainty. The reliability of occurrence records of species used to derive correlative niche models depends on the comprehensiveness of survey coverage, potential biases in recording presence or absence, observer skill at identification, and a host of other factors (62). Small sample size or inadequate spatial coverage decreases the statistical confidence of correlations underlying niche models and increases the uncertainty of extrapolating distributions to broader areas (60). Additionally, some surveys collect only presence data, whereas other surveys also document absences. Incorporation of absence data may strengthen a niche model (because where a species is not can reveal as much about its niche as where it is), but “absence” can mean a true absence or a failure to record a species that is actually present (“false absence”).

**Scale Uncertainties.** The choice of the spatial scale to be used in modeling depends on the scales of the available environmental data and the current species distributional data. At a very fine resolution (“grain”), distributions may not match environmental factors closely because behavioral interactions (territoriality, social attraction) may override habitat selection, whereas at the coarse resolution of a broad geographic range only the most general environmental relations may emerge in correlational analyses (26). SDMs conducted using large grid-cell sizes (coarser grain) may substantially overestimate potentially suitable areas in relation to those predicted by using a finer grid-cell size (63, 64), particularly if the data used to derive the initial distribution are sparse.

Mismatches in scale between the grain size of climate-model outputs, other environmental data, and the distributional data used as inputs to SDMs can amplify the uncertainties inherent in each of these data sets (65, 66). The effects of these scale-related uncertainties will differ depending on the scale of analysis. Some uncertainties may be averaged out if the grain size of predicted distributions is large (e.g., one is interested only in the overall geographic range of a species). On the other hand, the closer one gets to modeling fine-scale features, the more likely one may be able to capture the factors that determine the realized niche.

### Distributional Shifts of California Breeding Landbirds

Just because we are able to outline the assumptions and uncertainties in SDMs does not ensure that our modeling is immune to their effects. To illustrate the sorts of analyses that can be conducted by using niche modeling and SDMs and to assess how some of the assumptions and uncertainties can be addressed, we use our ongoing studies of shifts in the distributions of breeding landbirds with future climate change for California. We focused on California because it is a large, environmentally diverse state that may be especially vulnerable to the effects of climate change (67, 68) and because high-quality data on the distribution and occurrence of vegetation and bird species are available.

Using a correlational approach, we generated niche models for 60 focal bird species (see Table S1) representative of major habitat types in California (69). We used presence and absence data derived from point-count surveys at 16,742 locations in California. By restricting the bird occurrence information to data derived from point-count surveys connected to high-accuracy locational information, we increased the likelihood that our models captured the environmental space actually occupied by a species. We used two distribution modeling algorithms, maximum entropy [Maxent 3.2.1 (70)] and generalized additive models [GAM (52)], to project future bird distributions based on modeled associations with climate and vegetation (71) (methodological details are provided in *SI Text*). Current climate data were based on 30-year (1971–2000) monthly climate normals interpolated at an 800-m grid resolution by the PRISM Group (72). We reduced 19 standard bioclimatic variables ([www.worldclim.org/bioclim.htm](http://www.worldclim.org/bioclim.htm)) to a set of eight variables used in the final models (see Table S2). To improve the capacity of the SDMs to project changes in habitat relevant to birds, we included vegetation distribution, modeled for 12 vegetation classes (see Table S3) based on observed relations with climate, solar radiation, soil, and topography.

Because of California’s diverse climate and topography, we based our future distribution projections on newly available 30-km projections from a regional climate model, RegCM3 (73). Given the limited availability of GCM outputs at the appropriate temporal resolution, combined with the computational intensity of RCM runs, we had only two comparable sets of RCM projections available to us. These RCM runs were driven by output from two GCMs using the A2 emission scenario from the Intergovernmental Panel on Climate Change (IPCC) (47): (i) CCSM: the NCAR Community Climate System Model (CCSM

**Table 1. Mean change (percentage of pixels currently occupied) for bird species (*n*) characteristic of five vegetation types in California derived from four modeling approaches**

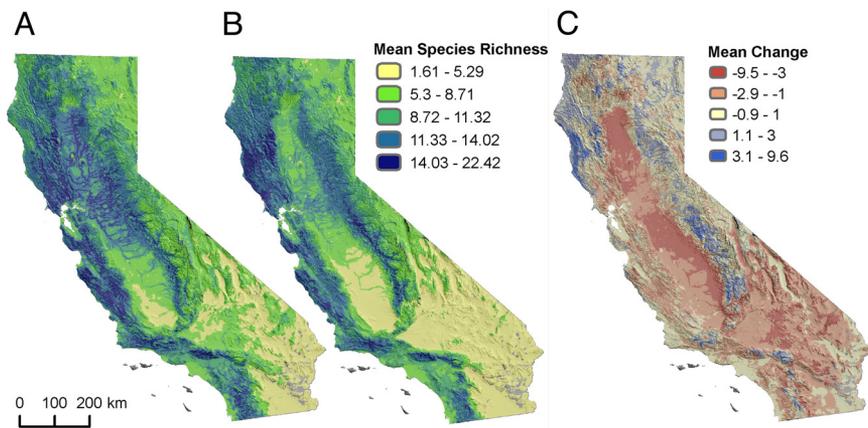
Vegetation		Change, % of pixels			
		GFDL/ GAM	CCSM/ GAM	GFDL/ Maxent	CCSM/ Maxent
Conifer ( <i>n</i> = 21)	Mean	−30	−31	−35	−43
	SD	42	31	33	23
	Min	−80	−96	−81	−91
	Max	106	43	71	26
Oak ( <i>n</i> = 19)	Mean	6	−1	7	−6
	SD	53	36	56	18
	Min	−71	−62	−51	−54
	Max	169	85	198	35
Grassland ( <i>n</i> = 3)	Mean	−63	−20	−63	−19
	SD	28	12	21	6
	Min	−89	−34	−76	−23
	Max	−33	−13	−39	−12
Riparian ( <i>n</i> = 7)	Mean	−32	−28	−40	−23
	SD	34	21	36	17
	Min	−70	−52	−78	−42
	Max	29	2	28	3
Scrub ( <i>n</i> = 19)	Mean	15	−2	−13	−11
	SD	71	41	48	26
	Min	−94	−65	−80	−62
	Max	202	85	113	35

The variance measures [standard deviation, SD, and range (minimum and maximum percentage change)] indicate the degree to which the species in the vegetation type differed from one another in overall change, and thus the magnitude of community turnover for places within that vegetation type.

3.0) (74) and (ii) GFDL: the Geophysical Fluid Dynamics Laboratory (GFDL) Climate Model (CM2.1) (75). Both CCSM and GFDL have good mean annual performance for temperature and precipitation (74, 75). Resulting climate projections do not represent a comprehensive range of model-projected future climates, but rather two plausible outcomes for California. Although the A2 emission scenario is considered a high-emission scenario by the IPCC (45), recent projections suggest that this is likely to be a conservative estimate of future emissions (76).

Most of the 60 species were projected to decrease in distribution within California by 2070 (Fig. 1). The four combinations of model algorithms and climate projections produced generally similar frequency distributions of mean species’ increases and decreases, although Maxent models projected somewhat greater losses than GAMs and GFDL-based projections were slightly more extreme than CCSM-based projections. The mean percent change projected for conifer-, riparian-, and grassland-associated species was negative across all four combinations of model algorithms and climate projections, whereas results for scrub- and oak woodland-associated species were more variable across models (Table 1). For all of the habitat types except grassland, however, there was a wide variety of projected distributional responses, both positive and negative, among species within the habitat type.

Even if the average probability of occurrence of a species across the state does not change with climate change, the species may still undergo a distributional shift. Geographic shifts across all species were summarized by summing pixel-level probabilities of occurrence to obtain an index of species richness at each pixel. Fig. 2 shows that the impacts of climate change on bird distributions are likely to differ substantially in different parts of the state, with the greatest projected increases in avian species richness along the north coast and mountain areas and greatest projected decreases in the northern Central Valley and desert



**Fig. 2.** Modeled current and future distributions of bird species richness in California for 60 focal species (A and B) and net change in species richness (C). Values are means for individual pixels derived from four climate scenario/distribution model algorithm combinations.

portions of the state. This demonstrates some of the anticipated coastward and upslope shifts in response to a warming climate, but also identifies more localized “hotspots” of change. These areas may warrant more detailed model analyses and targeted field-based observational or experimental studies to inform conservation or management actions.

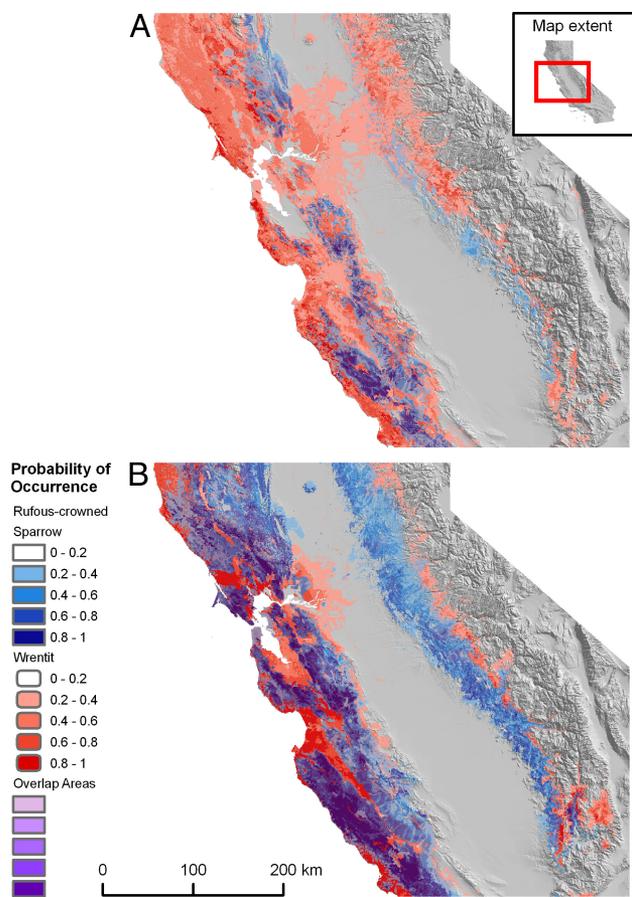
Changes in species richness in an area say nothing about how the species *composition* of the area may change. The responses of species to climate change were modeled independently of one another in accordance with species-specific niche models. As a result, species that currently do not co-occur in parts of their distribution may be found together in those areas in the future, or vice versa. For example, the distributions of two scrub-habitat species, wrenit (*Chamaea fasciata*) and rufous-crowned sparrow (*Aimophila ruficeps*) currently show only limited overlap in central California (Fig. 3A). Model analyses project that these species will be found together far more frequently in the future as the distributions of sparrows shift northward and wrenits shift toward coastal regions and upslope in the Sierra foothills (Fig. 3B).

To evaluate the potential for overall species turnover, we calculated a Jaccard index of community similarity between current and future species composition at the pixel level (13, 77, 78). This index is standardized with respect to species richness and therefore provides a relative measure of species turnover. Across models and climate projections, areas with the lowest community similarity (greatest projected change in community composition) over time tended to be in areas of rugged topography with steep gradients of environmental change (Fig. 4), although this was not always the case. This pattern suggests that shifts in distribution are not easily explained by environmental factors alone, but may be due to individualistic responses of species to climate change (e.g., Fig. 3). As co-occurring species respond to climate change in different ways, current assemblages of species will be reshuffled (79), creating new assemblages that may have no contemporary counterpart (40, 71).

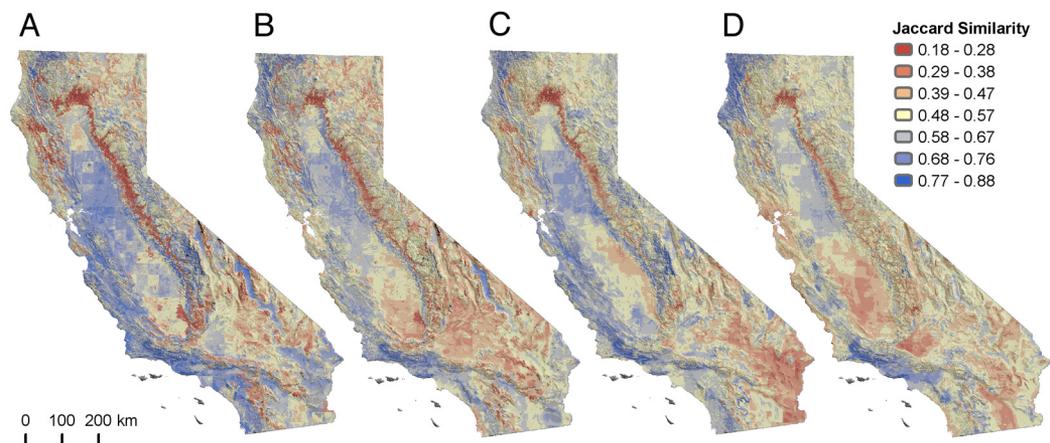
### Effects of Assumptions and Uncertainties

**Assumptions.** It is challenging to construct correlational niche models that include a sufficient number of relevant variables, while not including so many variables that the models are overfitted. It is also difficult to construct fine-scale projections, because environmental data at these finer scales are often unavailable. We attempted to make our model as fine-scale as possible, in several ways. We used the most fine-scale climate model projections available for California (30-km) and further downscaled them based on the best available current climate interpolations (PRISM; see *SI Text*) so that the resolution would

be most suitable for modeling habitat-level distributional responses. We included vegetation distribution as well as climatic variables in our models to improve the capacity to project habitat changes relevant to the bird species, and we modeled future vegetation distribution by incorporating information on soil and



**Fig. 3.** Modeled current and future distributions of wrenit (*Chamaea fasciata*) and rufous-crowned sparrow (*Aimophila ruficeps*) in the central portion of California. (A) Modeled current distributions (GAM), showing limited overlap between the species except at higher elevations in coastal mountains toward the south. (B) Projected future distributions (GDFL/GAM), showing increased co-occurrence of the species in coastal mountains, appearance of sparrows throughout the lower elevations of the Sierra Nevada mountains, and a shift in wrenits toward higher elevations.



**Fig. 4.** Pixel-level (800-m) patterns of similarity in California bird species assemblages between current and projected future modeled distributions for 60 focal species. Jaccard similarity index values were based on modeled species distributions using NCAR CCSM3.0, Scenario A2, 2038–2069, generalized additive models (GAM) (A), GFDL CM2.1, Scenario A2, 2038–2070, GAM (B), NCAR CCSM3.0, Scenario A2, 2038–2069, maximum entropy models (Maxent) (C), and GFDL CM2.1, Scenario A2, 2038–2070, Maxent (D).

topography as well as climate. Based on the frequent finding that birds respond more to the structure and form of vegetation than to floristic composition (80), we used general vegetation types rather than plant species to represent bird habitats. The mobility of birds also reduces the potential effects of dispersal limitations and increases the likelihood that suitable habitat will be occupied.

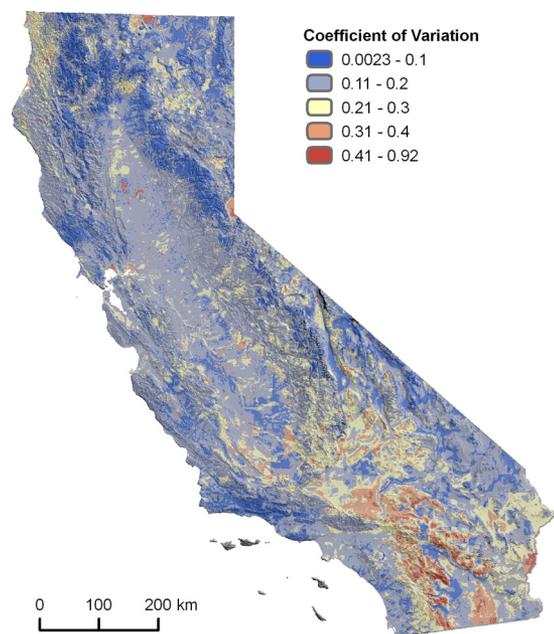
We were unable to address several other assumptions of niche models in our analyses. For example, we lacked information to consider demographic factors for all but a few species, and we had no data to include the potential effects of landscape structure on dispersal or metapopulation dynamics. In the absence of any information on adaptive or behavioral responses to environmental changes, we must also assume evolutionary stasis for the species we considered. Because we lacked any direct information to evaluate the effects of biotic interactions on the present or future distributions of species, we considered the species as independent entities. Addressing these issues should be a priority for next-generation SDMs.

**Uncertainties.** One way to reduce the uncertainty stemming from the differing projections of GCMs is to use several models in the analysis and then average the results—so-called ensemble models or consensus methods (23, 43, 81). This approach presumes that the different models are internally sound and incorporate accurate data; combining information from several uncertain or inadequate models may obscure underlying uncertainties that are actually magnified in the averaging process. Because of the limited availability of RCM projections, we did not employ a consensus approach (which often involves a dozen models or more) in the strict sense, but we did use two different RCM runs in association with two distributional algorithms to assess the variation in projections among models (Figs. 1 and 4). At a fine scale of spatial resolution there were clear differences among models (with some consistent differences between GAM and Maxent results), although the ranges of overall changes for the species associated with a given habitat type were broadly consistent among models (Table 1).

To reduce the uncertainty associated with the data on which the species-distribution projections are based, we used records from multiyear point-count surveys. These have the advantage of greater reliability in recording occurrence (and absence), but the disadvantage that such surveys are sparse from some areas (particularly the desert areas in the southeast). We also restricted our attention to reasonably widespread, common, and easily detected species, for which observations at point-count locations

within the species' range were relatively frequent. Analysis of elusive species or rare or endangered species would require the use of less systematic observations, which contain greater uncertainty.

What is really needed to assess overall uncertainty of SDM projections is an index that incorporates the various sources of uncertainty. As a first approximation, we have calculated the coefficient of variation of model projections for future bird species richness among the four modeling approaches for each pixel in our analysis (Fig. 5). This analysis highlights areas of greater uncertainty, which do not necessarily coincide with areas of greatest change in species richness or community composition. In our example, this uncertainty represents a combination of model and climate-projection uncertainties, which appear to be fairly similar in magnitude based on visual inspection of individual maps. Overall, the model-related uncertainty appears



**Fig. 5.** Geographic pattern in the uncertainty of model projections of future bird species richness in California, expressed as the coefficient of variation of projected future species richness at the 800-m pixel level among the four distribution model/climate scenario combinations (i.e.,  $n = 4$ ).

to be relatively low in most parts of the state, particularly in coastal areas and the lower elevations of the Sierra Nevada. Uncertainty is greater in a few scattered areas within the most arid parts of southern California. A comparison of the areas of greatest projected species loss in Fig. 2 with the locations of higher coefficients of variations shown in Fig. 5 indicates that the hotspots in the northwestern mountains and the middle Central Valley of California may be more certain to occur than those in some areas of the southeastern deserts.

## Conclusions

The most recent IPCC report (45) leaves little doubt that the changes in global climate that have already been set in motion will have major and accelerating effects on environmental systems, creating novel conditions that go well beyond our past experience. “Business as usual” will be an inadequate formula for future success in conservation and resource management. But to change how we approach conservation and management, we need some way of anticipating future environmental changes, of assessing which future pathways are most likely. Models are the most objective way to do this, and correlative SDMs are currently the most effective way of translating the projections of climate-change models into ecological consequences.

But models inevitably carry with them the baggage of simplifying assumptions and uncertainties. “Abandon hope all ye who enter here” could easily be the mantra of anyone undertaking ecological niche modeling, especially when using it to project future species distributions. Not using models to peer into the future, however, is not really an option. One could assume that the future will be like the present and that a business-as-usual approach will be sufficient, despite mounting evidence that the future will in fact be different. Or one could simply guess at what the future may hold and hope to be right.

In one sense, this is what models are: educated guesses about the future. By knowing the underlying assumptions, evaluating their potential effects, and incorporating additional detail into the models, we can narrow the guesses to define the more probable futures. Future efforts to incorporate demography, dispersal, landscape effects, biotic interactions, and the mechanistic underpinnings of species’ responses to biophysical factors will enhance the biological realism of SDMs. Even in their present form, however, the capacity of SDMs to use current information in conjunction with the projections of climate models can strengthen decision-making by conservationists and resource managers. Our projections of species richness changes (Fig. 2), for example, highlight areas that may be especially vulnerable to a loss of species and other areas that may experience a gain in species richness. Consideration of projections of areas that may contain similar species assemblages in the future (e.g., Fig. 4) can help to identify places in which similar management approaches may be effective. Such knowledge may be useful in determining where conservation investments should be made or where management or restoration efforts may yield the greatest benefits.

All of this raises the broader issue of how to deal with uncertainty in conservation and management. Decision-makers, managers, and practitioners like certainty, and they expect science to provide it. They want to be sure that the actions they take will have the desired effects. Yet they are seemingly confronted with increased uncertainty at every turn. The systems they aim to manage are complex and riddled with feedbacks, indirect effects, and nonlinearities, all of which erode certainty. The imperative to manage for future as well as present conditions adds to the challenge. Not only is the future always uncertain, but the approaches and tools we use to project the future are saddled with additional uncertainties.

There are no easy solutions to the uncertainty challenge, but we see three ways that may help conservationists and managers

deal with it. First, efforts should be made to develop ways of expressing quantitatively the level of uncertainty that is associated with the projections of SDMs. Is the definition of future hotspots of vulnerability to species loss depicted in Fig. 2, for example, certain enough to provide a foundation for targeting conservation investments? A spatially referenced analysis of the uncertainties accompanying these projections, such as the coefficient of variation (Fig. 5), can help to establish a context for interpreting and acting on such information. The coefficient of variation is only an initial and coarse measure of uncertainty, however; better approaches would help managers determine how much confidence to place in model projections.

Second, both managers and scientists should recognize that achieving the level of certainty usually deemed acceptable in scientific circles (e.g.,  $P < 0.05$ ) is not attainable in many current management situations, and is even less likely to be relevant to future projections. The situations that confront managers and conservationists are not given to analysis by tidy experimental designs that will yield statistical significance, and often there is too little time to conduct a rigorous study before decisions must be made. Aiming for a high level of certainty in such situations is impractical. Instead, managers must be satisfied with a level of certainty that is “good enough” to move forward, something between statistical confidence and having an unacceptable likelihood of making mistakes because of incomplete knowledge (82).

Third, the good-enough level of certainty depends on tradeoffs. If the costs of being wrong are large (e.g., declaring a species extinct when it still persists in undisclosed locations), then good enough requires a greater level of certainty than if the costs are small or the actions can be easily corrected. There may also be costs of taking no action when conditions demand a response (e.g., critical habitat for a species is rapidly disappearing). This will require some understanding not only of the uncertainty associated with projections or with actions and their outcomes, but also of the risks, costs, and benefits of alternative actions. This is the domain of ecological risk assessment (83, 84); there may be real value in integrating the formalisms of risk assessment with the projections of SDMs. In the end, determining how well conservation or management actions are working and whether the uncertainties include unforeseen factors that must be incorporated into the management equation requires targeted monitoring. In an increasingly uncertain world, implementing real adaptive management (85) will be essential.

So where does this leave us? Yes, SDMs currently contain many assumptions and uncertainties. There are ways of addressing some of the assumptions and reducing the uncertainties, however, and knowing what remains may enable us to focus our efforts in advancing niche-based modeling. Viewed at appropriate scales, the output of current SDMs can provide glimpses of probable futures that can be useful in conservation and resource management. The alternative is to ignore the future, which is really not an option.

**ACKNOWLEDGMENTS.** Terry Root provided frequent guidance. J.A.W. thanks David Wake, Elizabeth Hadly, and David Ackerly for the invitation to participate in the Sackler Colloquium and the opportunity to think once again about ecological niches. Funding for our work was provided by an anonymous donor to PRBO Conservation Science and by the Faucett Family Foundation. Data collection was supported primarily by the David and Lucille Packard Foundation, National Fish and Wildlife Foundation, U.S. Department of Agriculture Forest Service, Bureau of Land Management, National Park Service, Bureau of Reclamation, U.S. Fish and Wildlife Service, and the CALFED Bay-Delta Program. D.S. and D.J. were supported in part by the National Science Foundation (DBI-0542868); M.A.S. was supported in part by the National Science Foundation (ATM-0215934) and the California Energy Commission. Bird occurrence data were contributed by PRBO Conservation Science and research partners, the Klamath Bird Observatory, the U.S. Department of Agriculture Forest Service Redwood Sciences Laboratory, and the U.S. Geological Survey Breeding Bird Survey Program, through the work of countless field biologists, interns, and volunteers. This is PRBO contribution number 1687.

- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186.
- Morin X, Lechowicz MJ (2008) Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biol Lett* 4:573–576.
- Grinnell J (1917) The niche-relationships of the California Thrasher. *Auk* 34:427–434.
- Elton C (1927) *Animal Ecology* (Sedgwick and Jackson, London).
- Lack D (1947) The significance of clutch size. *Ibis* 89:302–352.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symp Quant Biol* 22:415–427.
- MacArthur RH (1972) *Geographical Ecology* (Harper & Row, New York).
- Wiens JA (1989) *The Ecology of Bird Communities, Vol 2: Processes and Variations* (Cambridge Univ Press, Cambridge, UK).
- Schoener TW (1989) in *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World*, ed Cherrert JM (Blackwell Scientific, Oxford), pp 79–113.
- Wiens JA (1977) On competition and variable environments. *Am Sci* 65:590–597.
- Simberloff D (1982) The status of competition theory in ecology. *Annales Zoologici Fennici* 19:241–253.
- Holt RD (1990) The microevolutionary consequences of climate change. *Trends Ecol Evol* 5:311–315.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* 102:8245–8250.
- Huntley B, Collingham YC, Willis SG, Green RE (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE* 3:e1439.
- Lawler JJ, et al. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecol Biogeogr* 12:361–371.
- Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2:1–10.
- Kearney M, Porter W (2009) Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecol Lett* 12:334–350.
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* 6:e325.
- Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biol* 12:2272–2281.
- Lawton JH (2000) in *The Ecological Consequences of Environmental Heterogeneity*, eds Hutchings MJ, John EA, Stewart AJA (Blackwell Scientific, Oxford), pp 401–424.
- Woodward FI, Beerling DJ (1997) The dynamics of vegetation change: Health warnings for equilibrium 'dodo' models. *Global Ecol Biogeogr Lett* 6:413–418.
- Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biol* 10:2020–2027.
- Rotenberry JT, Wiens JA (2009) Habitat relations of shrubsteppe birds: A 20-year retrospective. *Condor* 111:401–413.
- Loarie SR, et al. (2008) Climate change and the future of California's endemic flora. *PLoS ONE* 3:e2502.
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecol Lett* 3:349–361.
- Foden W, et al. (2007) A changing climate is eroding the geographical range of the Namib Desert tree aloe through population declines and dispersal lags. *Diversity and Distributions* 13:645–653.
- Jeschke JM, Strayer DL (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Ann NY Acad Sci* 1134:1–24.
- McLachlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conserv Biol* 21:297–302.
- Jetz W, Wilcove D, Dobson A (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* 5:e157.
- Pyke CR (2004) Habitat loss confounds climate change impacts. *Front Ecol Environ* 2:178–182.
- Sala OE, et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Gleason HA (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.
- Guisan A, et al. (2006) Making better biogeographical predictions of species' distributions. *J Appl Ecol* 43:386–392.
- Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Korber J-H (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecol Biogeogr* 16:754–763.
- Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol Biogeogr* 16:743–753.
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science* 315:640–642.
- Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Evol Systemat* 36:519–539.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenies and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* 58:1781–1793.
- Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ* 5:475–482.
- Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climatic fluctuation. *Proc Natl Acad Sci USA* 104:1278–1282.
- Root TL, et al. (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* 15:59–69.
- Beaumont LJ, Hughes L, Pitman AJ (2008) Why is the choice of future climate scenarios for species distribution modeling important? *Ecol Lett* 11:1135–1146.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Solomon S, et al. (Cambridge Univ Press, Cambridge, UK).
- Hayhoe K, et al. (2004) Emissions pathways, climate change, and impacts on California. *Proc Natl Acad Sci USA* 101:12422–12427.
- Wilby R, et al. (2004) *Guidelines for Use of Climate Scenarios Developed from Statistical Downscaling Methods* (Intergovernmental Panel on Climate Change), available at [www.ipcc-data.org/guidelines/dgm.no2.v1.09.2004.pdf](http://www.ipcc-data.org/guidelines/dgm.no2.v1.09.2004.pdf).
- Spak S, Holloway T, Lynn B, Goldberg R (2007) A comparison of statistical and dynamical downscaling for surface temperature in North America. *J Geophys Res Atmos*, 10.1029/2005JD006712.
- Wang T, Hamann A, Spittlehouse DL, Aitken SN (2006) Development of scale-free climate data for western Canada for use in resource management. *Int J Climatol* 26:383–397.
- Fowler H, Blenkinsop S, Tebaldi C (2007) Linking climate change modeling to impacts studies: Recent advances in downscaling techniques for hydrological modeling. *Int J Climatol* 27:1547–1578.
- Daly C, Smith JW, Smith JI (2007) High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. *J Appl Meteorol* 46:1565–1586.
- Hastie TJ, Tibshirani RJ (1990) *Generalized Additive Models* (Chapman & Hall, London).
- Pearson RG, Dawson TP, Berry PM, Harrison PA (2002) SPECIES: A spatial evaluation of climate impact on the envelope of species. *Ecol Model* 154:289–300.
- Stockwell DRB, Peters DP (1999) The GARP modelling system: Problems and solutions to automated spatial prediction. *Int J Geogr Inform Syst* 13:143–158.
- Carpenter G, Gillson AN, Winter J (1993) DOMAIN: A flexible modeling procedure for mapping potential distributions of plants and animals. *Biodivers Conserv* 2:667–680.
- Busby JR (1991) in *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*, eds Margules CR, Austin MP (Commonwealth Scientific and Industrial Research Organization, Collingwood, Victoria, Australia), pp 64–68.
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Appl* 19:231–259.
- Elith J, et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Lawler JJ, White D, Neilson RP, Blaustein AR (2006) Predicting climate-induced range shifts: Model differences and model reliability. *Global Change Biol* 12:1568–1584.
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- Thuiller W, Araújo MB, Lavorel S, Kenkel N (2003) Generalized models vs. classification tree analysis: Predicting spatial distributions of plant species at different scales. *J Veg Sci* 14:669–680.
- Scott JM, Heglund PJ, Morrison ML (2002) *Predicting Species Occurrences: Issues of Accuracy and Scale* (Island, Washington, DC).
- Jetz W, Krefth H, Ceballos G, Mutke J (2008) Global associations between terrestrial producer and vertebrate consumer diversity. *Proc Biol Sci* 276:269–278.
- Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: Implications for conservation planning under climate change. *Biol Lett* 5:39–43.
- Wiens JA, Bachelet D (2009) Matching the multiple scales of conservation with the multiple scales of climate change. *Conserv Biol*, in press.
- Root TL, Schneider SH (1993) Can large-scale climatic models be linked with multiscale ecological studies? *Conserv Biol* 7:256–270.
- Lenihan J, Bachelet D, Neilson R, Drapek R (2008) Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Climatic Change* 87:215–230.
- Luers AL, Cayan DR, Franco G, Hanemann M, Croes B (2006) *Our Changing Climate. Assessing the Risks to California* (California Energy Commission, Sacramento, CA), publication CEC-500-2006-077, available at [www.climatechange.ca.gov](http://www.climatechange.ca.gov).
- Chase M, Geupel GR (2005) in *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference, General Technical Report PSW-GTR-191*, eds Ralph CJ, Rich TD (U.S. Dept Agriculture Forest Service, Albany, CA), pp 130–142.
- Phillips SJ, Dudik M (2008) Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Stralberg D, et al. (2009) Re-shuffling of species with climate disruption: A no-analog future for California birds? *PLoS ONE* 4:e6825.
- Daly C, Neilson RP, Phillips DL (1994) A statistical topographic model for mapping climatological precipitation over mountainous terrain. *J Appl Meteorol* 33:140–158.
- Pal JS, et al. (2007) Regional climate modeling for the developing world: The ICTP RegCM3 and RegCM2. *Bull Am Meteorol Soc* 88:1395–1409.
- Collins WD, et al. (2006) The Community Climate System Model Version 3 (CCSM3). *J Climate* 19:2122–2143.
- Delworth TL, et al. (2006) GFDL's CM2 global coupled climate models. Part I: formulation and simulation characteristics. *J Climate* 19:643–674.
- Sokolov AP, et al. (2009) Probabilistic forecast for 21st century climate based on uncertainties in emissions (without policy) and climate parameters. *J Climate*, in press.
- Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biol* 8:390–407.
- Peterson AT, et al. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 41:626–629.
- Root TL, Schneider SH (2002) in *Wildlife Responses to Climate Change: North American Case Studies*, eds Schneider SH, Root TL (Island, Washington, DC), pp 1–56.
- Rotenberry JT (1985) The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia* 67:213–217.
- Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography* 28:693–695.
- Wiens JA (2008) Uncertainty and the relevance of ecology. *Bull British Ecol Soc* 39:47–48.
- Burgman M (2005) *Risks and Decisions for Conservation and Environmental Management* (Cambridge Univ Press, Cambridge, UK).
- Wiens JA (2007) Applying ecological risk assessment to environmental accidents: Harlequin ducks and the Exxon Valdez oil spill. *Bioscience* 57:769–777.
- Williams BK, Szaro RC, Shapiro CD (2007) *Adaptive Management: The U.S. Department of the Interior Technical Guide* (Adaptive Management Group, U.S. Department of the Interior, Washington, DC).