The push and pull of climate change causes heterogeneous shifts in avian elevational ranges

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Abstract

Projected effects of climate change on animal distributions primarily focus on consequences of temperature and largely ignore impacts of altered precipitation. While much evidence supports temperature-driven range shifts, there is substantial heterogeneity in species' responses that remains poorly understood. We resampled breeding ranges of birds across three elevational transects in the Sierra Nevada Mountains, USA, that were extensively surveyed in the early 20th century. Presence–absence comparisons were made at 77 sites and occupancy models were used to separate significant range shifts from artifacts of false absences. Over the past century, rising temperature pushed species upslope while increased precipitation pulled them downslope, resulting in range shifts that were heterogeneous within species and among regions. While 84% of species shifted their elevational distribution, only 51% of upper or lower range boundary shifts were upslope. By comparison, 82% of range shifts were in a direction predicted by changes in either temperature or precipitation. Species were significantly more likely to shift elevational ranges than their ecological counterparts if they had small clutch sizes, defended all-purpose territories, and were year-round residents, results that were in opposition to *a priori* predictions from dispersal-related hypotheses. Our results illustrate the complex interplay between species-specific and region-specific factors that structure patterns of breeding range change over long time periods. Future projections of increasing temperature and highly variable precipitation regimes create a strong potential for heterogeneous responses by species at range margins.

Keywords: birds, California, climate change, elevational range shift, occupancy models, precipitation, Sierra Nevada

Introduction

Global climate change is expected to shift the distributions of organisms, with predicted consequences of large-scale extinctions (Thomas *et al.*, 2004; Colwell *et al.*, 2008; La Sorte & Jetz, 2010; Sinervo *et al.*, 2010) and formation of novel assemblages (Roy *et al.*, 1996; Williams, 2007; Stralberg *et al.*, 2009). With few exceptions (e.g., Bonebrake & Mastrandrea, 2010; Crimmins *et al.*, 2011), the focus has been on attribution of poleward and upslope shifts of species ranges to increasing temperature (Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Root *et al.*, 2003; Moritz *et al.*, 2008; Chen *et al.*, 2011). However, this belies a more complex reality; up to 25% of the species examined worldwide have shifted ranges equatorially or downslope, and ranges of an additional 10–30% of species have not shifted

(Parmesan & Yohe, 2003; Chen *et al.*, 2011). A limited understanding of the complexities underlying these heterogenous, species-specific responses to climate change prevents accurate predictions of response to future climate change (Buckley *et al.*, 2010).

Numerous hypotheses have arisen seeking to explain variation among species' responses to climate change. Downslope movements could be caused by climate-induced changes to competitive species interactions (Hughes, 2000; Lenoir *et al.*, 2010), land-use changes (Archaux, 2004), changes in nontemperature environmental gradients (Tingley *et al.*, 2009; Zimmermann *et al.*, 2009; Crimmins *et al.*, 2011), and stochastic fluctuations in population size (Lenoir *et al.*, 2010). Nonmovement, or range stability, may result from adaptation of local populations to new climates (Rodríguez-Trelles & Rodríguez, 1998; Parmesan *et al.*, 2005), an inability to disperse (Davis *et al.*, 1998), an insufficient amount of climate change to push species out of their fundamental niche (Tingley *et al.*, 2009), or a temporal lag in movement response (Svenning *et al.*, 2008). Linking these hypotheses are the different intrinsic ecological traits

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held by diverse species assemblages. Past studies had moderate success relating species-specific patterns of range movements to life history and species' traits, such as body size, habitat requirements, and fecundity (Perry *et al.*, 2005; Moritz *et al.*, 2008; Pöyry *et al.*, 2009). In most cases, however, the statistical power to determine these relationships was greatly limited (Angert *et al.*, 2011), and results may have been obscured by the effects of false absences on occurrence data (Link & Nichols, 1994; Kéry, 2004; Kéry *et al.*, 2006). Given the multitude of mechanisms and processes potentially driving range change, temporally and spatially replicated surveys across taxa are needed to test these hypotheses (Parmesan *et al.*, 2005).

We quantified the impacts of temperature and precipitation changes over the last century on ranges of breeding birds along three broad elevational transects located primarily in US National Park and US Forest Service lands in the Sierra Nevada mountains of California (Fig. 1a). Systematic surveys were originally done 80–100 years ago by Joseph Grinnell and colleagues. Although annual minimum and maximum temperatures have increased on average between 1 and 2 °C throughout the Sierra Nevada over the last century (Bonfils *et al.*, 2008), there is substantial spatial variation in both temperature and precipitation change (Fig. 1b). Substantial warming occurred in the southern and central Sierra Nevada, while the northern portion experienced either marginal warming (low elevations) or local cooling (high elevations). Precipitation generally increased over the same time period, with the greatest change in the north and at higher elevations (Fig. 1b).

Temperature and precipitation changes over the past century in many parts of the Sierra Nevada yield opposing expectations as to whether species should move upslope or downslope if species shift distributions to track their climatic niche (Grinnell, 1917; Brown *et al.*, 1996; Tingley *et al.*, 2009). Increased temperature should push species upslope, but increased precipitation should pull them downslope. This arises because precipitation generally increases with elevation in montane systems, but temperature decreases (Fig. 1b). As a result, temporal increases in precipitation will shift precipitation-based climatic niches downslope, whereas warming will shift thermal-based climatic niches upslope. Topography and localized weather conditions can create nonlinearities in these general patterns, leading to variable and local effects of climate on species. To consider the potential for temperature and precipitation to alternatively push and pull breeding bird distributions in alternate directions, we formulated species- and limit-specific predictions for how upper- and lower-elevation boundaries should shift independently over time, as determined separately by changes in average mean temperature and precipitation. Expectations were derived from the difference in elevation between each survey site and the nearest modern-climatic neighbor within each region (see *Methods*, Table S1). The majority of sites have modern-temperature nearest neighbors at higher elevations, as expected given the average warming trend, but many sites have modern precipitation nearest neighbors at lower elevations (Fig. 1c). Expected range shifts from temperature and precipitation changes over the past century were in opposing directions at 60% of survey sites, primarily at higher elevations (Fig. 1d).

Given the recent climatic history within the Sierra Nevada, our goals were to: (1) test for an overall upward shift in elevational range expected by average warming; (2) test whether directional shifts in elevation were better explained by site-specific temperature or precipitation changes; and (3) determine if species' traits can explain variation in movement responses. To quantify range change from historical data, we conservatively excluded shifts that may be due to false absences or that represent normal, minor range fluctuations. In addition, we hypothesized that dispersal- and colonization-related traits should be positively related to range movements (Angert *et al.*, 2011), including migration during the nonbreeding season, large clutch size, large home range size, small body size, low territoriality, and a generalist diet.

Materials and methods

Collection and sampling of field data

Bird observations were collected as part of the Grinnell Resurvey Project (Moritz *et al.*, 2008; Tingley *et al.*, 2009), a multiyear endeavor to revisit historical vertebrate sampling sites throughout the state of California. A total of 77 historical survey sites were revisited, as well as seven additional sites that were sampled only contemporarily. Sites were distributed across three elevational cross-sections of the Sierra Nevada mountain range, from north to south: Lassen, Yosemite, and Southern Sierra (Fig. 1a). All sites contained characteristic 'west-slope Sierran' vegetation communities (i.e., Central Valley riparian, oak woodland, Sierran mixed conifer, yellow pine forest, lodgepole and true fir forests, and alpine) and excluded Great Basin and Sonoran desert habitat. Elevational ranges were 80–2751 m for Lassen sites, 65–3226 m for Yosemite sites, and 61–3356 m for Southern Sierra sites. Over 87% of survey sites were located on permanently protected lands, with 66% of sites owned by the federal government.

Historical bird observations were conducted between 1911 and 1929 as part of regular biotic surveys by Joseph Grinnell, Tracy Storer, and seven other researchers from the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (Grinnell & Storer, 1924; Grinnell *et al.*, 1930). Survey effort
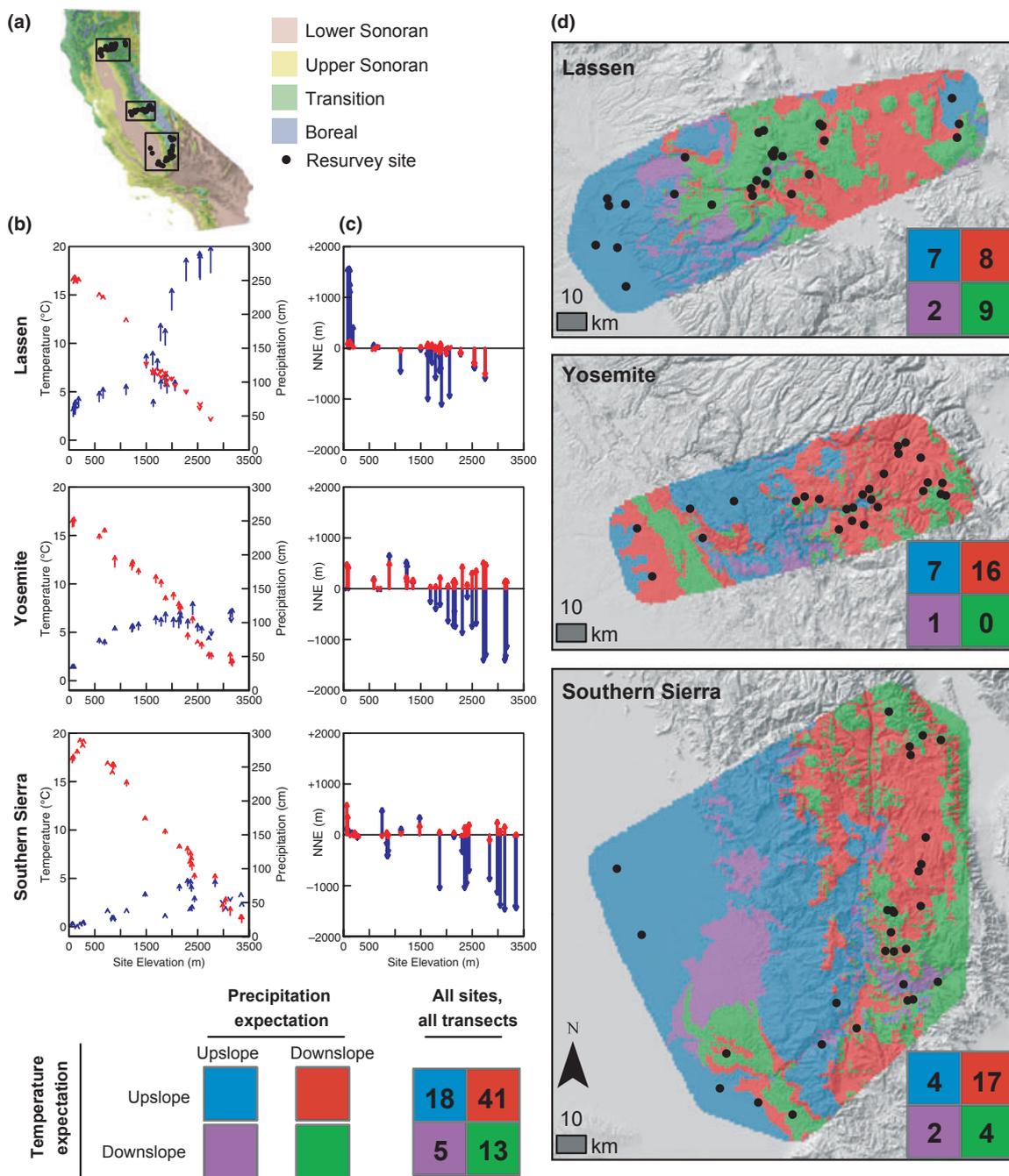
Fig. 1 Twentieth century climate change and resultant expected range shifts for three resurveyed regions of the Sierra Nevada of California. (a) Elevational transects showing locations of resurvey sites superimposed on topography and Grinnell's life zones. (b) Changes in average annual temperature (red arrows) and precipitation (blue arrows) between 1900–1930 and 1980–2006 for survey sites in each region. Arrows point from the average historical climate at a site to the average modern climate at the site. (c) Differences between the elevation of each site and the nearest neighbor elevation based on 20th century changes in temperature (red arrows) and precipitation (blue arrows). Positive differences in nearest neighbor elevation (arrows above the black line) indicate that a species at a particular site would need to shift upslope to stay as close as possible to historic climatic average conditions at that site. (d) Agreement and disagreement between temperature- and precipitation-based nearest neighbor elevation change predictions for survey sites (black dots) in each region. The number of survey sites with concordant (blue and green, see legend) and discordant (red and purple, see legend) predictions are shown as numbers within each set of boxes. The number of concordant and discordant sites summed across all regions (located next to the legend) illustrates that species at 60% of sites ($n = 77$) experienced opposing climatic pressures from temperature and precipitation over the 20th century.

was focused on different geographical areas for certain years, with primary sampling periods being: 1924–1928 for Lassen; 1915–1919 for Yosemite; and 1911 for Southern Sierra. Historical surveys were taken opportunistically using a precursor of the line-transect method (Bibby *et al.*, 2000). Surveys listed all species encountered, providing reliable detection/nondetection data. All survey observations, as well as details on location, extent, duration, and weather, were recorded in field notebooks held at the MVZ (available online at http://bscit.berkeley.edu/mvz/volumes.html). A total of 266 historic surveys were used as baseline data on avian occurrence, with each of the 77 sites surveyed up to 17 times (median = 3 visits).

Modern resurveys were done using point counts along a line transect that followed, as closely as possible, the same survey route taken by historical observers. When field notes lacked details to establish exact historic routes, routes were placed following named geographical features in habitats matching those described in the field notes to achieve our goal of determining whether sites in an elevation band were occupied. Whenever possible we matched habitat descriptions in the original field notes. Sites with mixed land-use were subject to the same class of current and historical land-use (e.g., grazing or agriculture). For resurveys we used variable-distance point counts (Ralph *et al.*, 1995) lasting 7 min. Observation points were separated by a minimum of 250 m and varied in number per site depending on the extent of the historical route (median = 10 points over 2.5 km). Five trained primary observers collected data as part of 1- or 2-person survey teams with temporal sampling as follows: Lassen, 2006–2007; Yosemite, 2003–2004; and Southern Sierra, 2008–2009. A total of 251 modern surveys were conducted at 84 sites, with each site surveyed a maximum of 5 times (median = 3). All modern occurrence records are archived online in the MVZ's collections database (http://arctos.database.museum/), and are available by arrangement through the authors.

Bird surveys characterized elevational ranges of species during the breeding season. Historically, survey dates ranged between 25 March and 2 October, with 87% conducted between 1 May and 31 August. Modern resurveys visited sites around the same time as historical surveys, but were concentrated within the breeding season (dates ranged between 3 May and 25 August). Sites were typically surveyed within one breeding season (79% historic, 80% modern), and most were surveyed within 1 week (historic 66%, modern 53%); the remaining sites (20–21%) were surveyed across two or more years. Further information on the temporal structure of surveys during both time periods is presented in Appendix S1. As both migrating birds and postbreeding dispersal of juveniles could potentially bias inference on breeding ranges for both time periods, observations were excluded from analysis if either the individual detected was a juvenile or was clearly in migration (as determined by behavior, plumage, and expert knowledge).

Focal species selection

A total of 223 bird species were recorded in at least one survey, but not all species occurred across all three regions. We created independent focal species lists for each region, including species detected at a minimum of 10% of sites within both eras. We additionally excluded all nonpasserines, as most were observed sporadically, except those in five families: Odontophoridae, Phasianidae, Columbidae, Trochilidae, and Picidae. Our final region-specific species list tallied 78 species for Lassen, 78 species for Yosemite, and 73 species for Southern Sierra. Combining the three regions resulted in 99 focal species, of which 53 were common to all region lists.

Modeling of elevational ranges

We used a 'single-season' occupancy model probability framework (MacKenzie *et al.*, 2003, 2006) to simultaneously estimate a probability of detection (p) and a probability of occupancy (ψ) for each species. To explore whether occupancy changed over time, we used an 'unpaired-site' model (Tingley & Beissinger, 2009), which tests for a temporal ('era') effect as a covariate of ψ within a single-season model. To account for both heterogeneity in detection and false absences, we tested six parameterizations of p models using two different covariates. The variable era allowed the probability of detection to differ by time period (historic vs. modern), while Julian day (jday, with linear and squared effects) was used to test if p changed over the survey season. Other candidate variables were considered (including habitat and intraera observer-specific effects), but preliminary analyses concluded they were much less important in explaining heterogeneity in detectability (Appendix S1), so were not included in candidate models to reduce model set complexity (Burnham & Anderson, 2002). Continuous covariates were standardized to a mean of zero and standard deviation of one. All combinations of era, jday, and $jday^2$ were used, in addition to a null (intercept-only) model. The detection model employed is described as:

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_1 \text{era}_j + \alpha_2 \text{jday}_k + \alpha_3 \text{jday}_k^2$$

defining a probability of detection (p) for species i, at site j, for survey k.

Following Moritz *et al.* (2008), single-season occupancy parameterizations sought to examine how occupancy changed over time (era), over elevation (*elevation* and *elevation*^{2}), and, in this case, among the three regions (defined by two dummy variables, *R1* and *R2*). As sites consisted of survey routes that covered a range of elevations, we assigned a single elevation value to each site defined by the mean elevation of point count stations comprising each site. We tested 25 different ψ parameterizations, which included all combinations of these covariates along with all two- and three-way interaction terms and a null (intercept-only) model (full model set listed in Table S2). Our final model set combined all 6 p parameterizations with all 25 ψ parameterizations, resulting in 150 model combinations of p and ψ that were run for each species. Unconditional, model-averaged values of $p_{i,j,k}$ and $\psi_{i,j}$ were calculated using AIC weights (w_i) of each model, resulting in one composite model for each species (Burnham & Anderson, 2002; Moritz *et al.*, 2008). All occupancy models were run in R version 2.13 (R Development Core Team, 2011) based on code modified from Royle & Dorazio (2008).

Measurement of elevational ranges and estimation of change

We used a combination of restrictions to conservatively estimate significant range change at elevational limits of distributions. First, we used a P_{fa} (probability of false absence) test on both lower- and upper-elevation range boundaries within each region to eliminate apparent shifts that could be due to imperfect detection of individuals at range margins. P_{fa} calculates the probability that a species was present but not detected at a set of sites at a range limit (Moritz *et al.*, 2008; Tingley & Beissinger, 2009), and can be expressed as:

$$P_{fa} = \prod_{j=1}^{m}(1 - p_j^*) = \prod_{j=1}^{m}\prod_{i=1}^{n}(1 - p_{ij})$$

where p_{ij} is the probability of detection at the ith survey of site j, and p_j^* is the probability of detecting the species over n surveys at site j. The probability of false absence is then calculated across m sites with nondetections to estimate the chance the species was present at all of those sites and escaped detection. Range limit shifts with a $P_{fa} \leq 0.05$ were statistically significant. In addition, we considered statistically significant results of P_{fa} tests to be ecologically meaningful if the magnitude of the shift was greater than 10% of the species' historical elevational range within a region (e.g., if a historical range was from 500 to 1500 m, then range change at either limit would need to be greater than 100 m) following Moritz *et al.* (2008). Plots of historic and modern occupancy and the results of P_{fa} tests for each species analyzed appear in Appendix S2. Simulations of our ability to detect actual range shifts given our sampling structure suggest that our methods are highly conservative, with a Type I error rate of approximately 1% (see Appendix S1). This conservatism is also robust to potential violations of the closure assumption within resurveys at sites – a possibility that has been suggested to bias occupancy results (Rota *et al.*, 2009). While our restrictive conditions for assigning elevational range change likely underestimate the true number of range shifts (simulations presented in Appendix S1), our conservative methods are warranted given our inferential goals as well as the difficulty of working with historical data (Tingley & Beissinger, 2009).

Climatic nearest neighbor predictions

Trends in average annual climate (Fig. 1b) were ascertained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly *et al.*, 2002). We used surfaces with 1 × 1 km, or 30 arc-second, spatial resolution (received 26 January 2009 from C. Daly) to quantify both historical (1910–1930) and modern (1989–2009) average annual temperature and precipitation at each of our survey locations. Average annual temperature at our sites was highly correlated in both time periods with other temperature variables (max annual temperature: ρ = 0.97; min annual temperature: ρ = 0.96), and average annual precipitation was similarly highly correlated with other precipitation variables (precipitation of wettest month: ρ = 0.98; precipitation of driest month: ρ = 0.73).

Estimation of nearest neighbor elevations followed established methods (Ackerly *et al.*, 2010) by measuring the Euclidian distance between the historic climate (temperature or precipitation) at a single site and the modern climate at a regional set of sites (Fig. S1). The regional set comprised all 1 × 1 km PRISM grid cells within a geographic area defined by a minimum convex polygon plus 20 km buffer surrounding all survey localities in a region. Nearest climatic neighbors were identified by measuring the climatic distance between modern climate cells and the historic climate at a survey site (Fig. S1a). The climatically nearest 5% of cells were pooled and their elevations were averaged, to account for local heterogeneity in climate and elevation (Fig. S1b). Survey sites were only compared to climates of cells within the same region. Comparing the elevation of each site and the average elevation of its 5% modern-climatic nearest neighbors allowed the creation of site-specific predictions of elevation change for each survey site (Figs. 1c, S1b) and for every grid cell within each region (Fig. 1d). Upper- and lower-limit predictions for each species were based on the predictions for the actual sites where a species had its historical upper and lower limit.

Mixed-model hypothesis testing

Generalized Linear Mixed Models (GLMM) were used for two analyses of patterns of range change. First, we sought to understand the environmental factors related to upslope vs. downslope movement patterns. A binary response variable was used to indicate whether a range limit had moved upslope (value = 1) or downslope (value = 0) for species that had significant range shifts. All range limits, regions, and species were pooled together. Explanatory variables used included: (1) range limit (categorical: upper or lower); (2) survey region (categorical: Lassen, Yosemite, Southern Sierra); (3) temperature-based predictions of upslope or downslope movement based on nearest neighbor analysis (categorical: upslope or downslope); (4) precipitation-based predictions of movement based on nearest neighbor analysis (categorical: upslope or downslope); and (5) regional population trend for species in the second half of the 20th century (continuous: percent change in population per year, signs reversed for lower limit data). Population trend values were derived from Sierra Nevada-specific estimates of the North American Breeding Bird Survey for 1966–2008 (Sauer *et al.*, 2008), a continent-wide annual survey of breeding bird populations.

Second, GLMMs were used to examine how well individual species' traits explained whether or not species moved, regardless of direction. Whereas movement direction may be related to climate change, the ability and motivation to move may be a species-specific trait. Life history data were compiled for all species based on accounts from *The Birds of North America Online* (Poole, 2005). We tested: (1) migratory status (three levels: permanent resident; short-distance migrant; and long-distance migrant); (2) mean mass of breeding adult (average of male and female masses of California subspecies, when available); (3) territory type (i.e., whether an all-purpose 'Type-A' (Nice, 1941) territory is defended); (4) mean home range size of breeding individuals; (5) mean clutch size of

females; and (6) diet breadth (i.e., omnivore vs. specialized diet). Data on all trait measures were available for 86 of the 99 focal species (Table S3). These six life history traits were included in a GLMM analysis of the probability of an elevational range shift combined with (7) elevation zone, as determined by the historical classification of life zones in Grinnell's monographs (Grinnell & Storer, 1924; Grinnell *et al.*, 1930) following Moritz *et al.* (2008). In a two-part process, each species trait was first added as a factor on its own and then in combination with elevation zone. Subsequent models tested multiple traits by adding traits individually in the order ranked by the initial AIC scores. Traits were added in this forward stepwise process until additional traits no longer improved AIC scores. All GLMM models were fit using a logit link and included species identity as a random effect. All models were run in R (R Development Core Team, 2011) using the package 'lme4' (Bates & Maechler, 2011).

Results

Significant changes in one or both range limits were found for 84% of bird species across all regions of the Sierra Nevada, but the direction of change was heterogeneous (46% and 53% of shifts were upslope for lower

and upper limits, respectively), as were responses across the three regions (Fig. 2). Upward shifts ranged from 161 to 1320 m for lower limits and 218 to 2503 m for upper limits, whereas downward shifts ranged from 113 to 1557 m for lower limits and 127 to 1567 m for upper limits. The largest range shift in any direction was observed in the Savannah Sparrow (upper limit shifted up 2503 m in Southern Sierra). Species that shifted an elevational range limit upslope >1 km in any region included American Goldfinch, Downy Woodpecker, Pine Siskin, Black Phoebe, Bushtit, Mourning Dove, Purple Finch, Red-winged Blackbird, White-breasted Nuthatch, Chipping Sparrow, Lark Sparrow, Northern Mockingbird, Song Sparrow, and Western Meadowlark. Species that shifted an elevational range limit downslope >1 km in any region included Downy Woodpecker, Black-chinned Hummingbird, Bewick's Wren, House Finch, American Robin, and Violet-green Swallow. Appendix S2 shows results for all species and regions.

The naïve expectation of 'moving up' was supported for bird species in the Yosemite region, which expanded their upper limits upslope (one-sided bino-
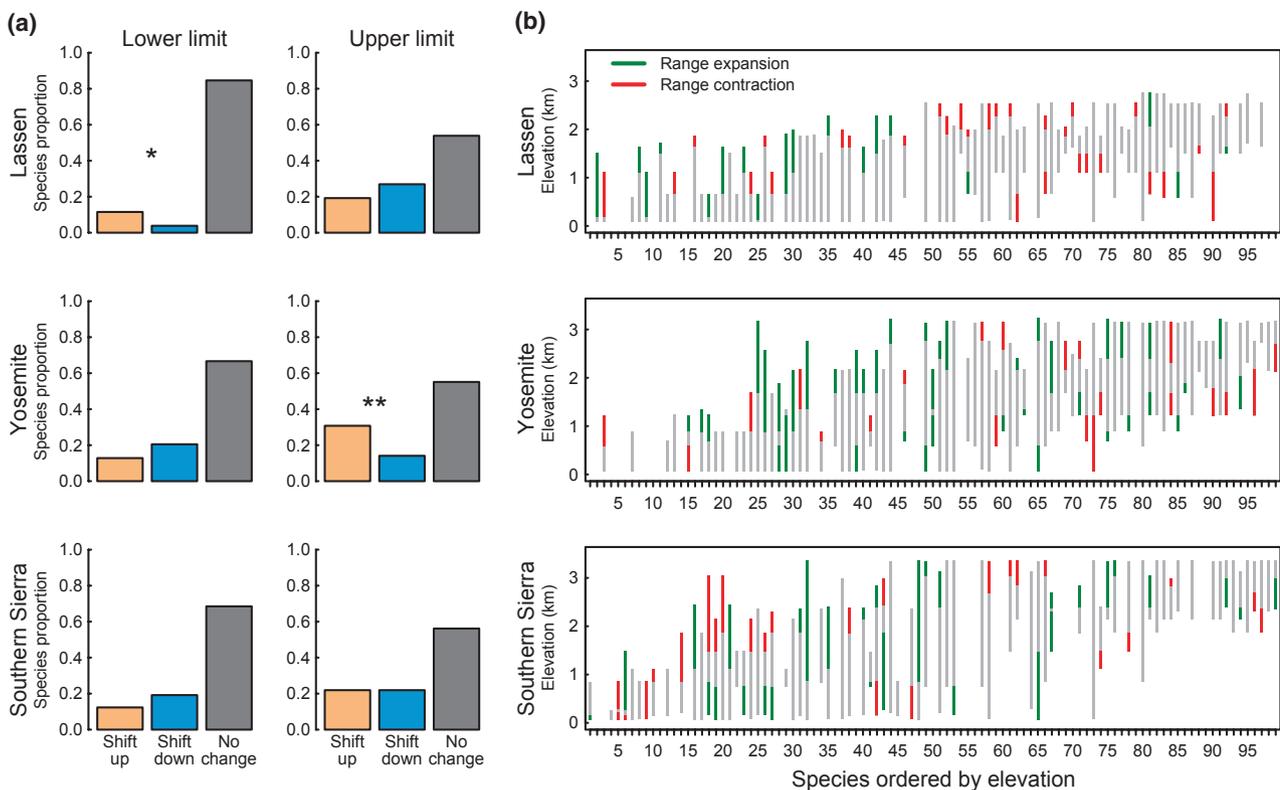
Fig. 2 Upslope and downslope range shifts by birds over 80–100 years. (a) Significant elevation change in species range by limit for three regions in the Sierra Nevada. Species shifted upslope more than downslope for two region-limit comparisons (*$P < 0.1$, **$P < 0.05$). (b) Graphical summary of all range shifts for each species ($n = 99$), showing the historical range (gray bar), plus expansions (or colonizations; green) or contractions (or extinctions; red) over the ensuing century. Species numbers (*x*-axis) correspond to the species list in Table S1.

Table 1 Generalized linear mixed models examining the pattern of upslope and downslope movements of 99 bird species in three regions of the Sierra Nevada, California, over the last century

Model name[*]	K	log $\mathcal{L}$	AIC	ΔAIC[†]	w_i
limit + temp + precip	5	−106.6	223.2	0.0	0.23
limit + precip	4	−107.8	223.6	0.4	0.19
limit + temp + precip + pop. trend	6	−106.4	224.7	1.6	0.11
limit + precip + pop. trend	5	−107.5	225.0	1.8	0.09
limit + region + temp + precip	7	−105.6	225.1	2.0	0.09
limit + region + temp + precip + pop. trend	8	−105.3	226.7	3.5	0.04
precip	3	−110.5	226.9	3.7	0.04

*Explanatory variables hypothesized to affect whether a species shifted upslope or downslope included the range limit being tested ('limit'; i.e., upper range limit or lower range limit), the region of the Sierra Nevada ('region'; i.e., Lassen, Yosemite, or Southern Sierra), the expected upslope or downslope shift based on the temperature-based ('temp') or precipitation-based ('precip') nearest neighbor analysis, and species-specific population trend derived from regional survey data 1966–2008 ('pop.trend'). Explanatory factors were modeled as fixed effects, and all models included species as a random effect.
†Only models with ΔAIC values less than 4 (indicating strongly supported models) are shown (see Table S4 for all models).

mial test, $n = 35$, $p = 0.02$), and was marginally supported for species in the Lassen region that contracted their lower range limits upslope (one-sided binomial test, $n = 12$, $p = 0.07$). Across all regions, however, neither upper nor lower range limits significantly shifted upslope more frequently than downslope (one-sided binomial tests, upper: $n = 103$, $p = 0.28$; lower: $n = 61$, $p = 0.78$). Of the 53 species analyzed in all three regions, only 5 species significantly shifted in the same direction throughout the Sierra Nevada for a single range metric: Red-breasted Sapsucker, Fox Sparrow, Lazuli Bunting, and Spotted Towhee shifted upslope in all three regions while Ash-throated Flycatcher shifted downslope in all three regions.

The direction of shifts in elevational range limits between 1911 and 2009 were best explained by accounting for movement expectations based on both temperature and precipitation (Table 1). The best-fitting GLMM model of directional shifts included both temperature- and precipitation-based nearest neighbor expectations. Summing AIC weights across models (Burnham &

Anderson, 2002), the weight of evidence was nearly twice as strong for precipitation-based expectations (cumulative $w_i = 0.92$) as temperature-based expectations (cumulative $w_i = 0.56$). However, models with either temperature alone (cumulative $w_i = 0.04$) or precipitation alone (cumulative $w_i = 0.39$) were not as strongly supported as models that included both (cumulative $w_i = 0.52$), suggesting that localized range shifts may result from only one climatic factor, but that both temperature and precipitation influence shifts over a larger geographic range.

Range limit was an important factor affecting direction of change (cumulative $w_i = 0.84$), with upper limits significantly more likely to shift upslope than lower limits. Region received little model support (cumulative $w_i = 0.22$) after controlling for site-specific climatic trends using nearest neighbor expectations. Moreover, range shifts seemed unaffected by late 20th century population trends of species, which had less support across all models than climate (cumulative $w_i = 0.32$). Thus, elevational range expansions or contractions were primarily related to climate-based expectations and were not confounded by regional population changes (Thomas & Lennon, 1999).

Although avian ranges did not shift upslope consistently, they did shift in accord with climate-driven responses. Eighty-two percent of all range shifts were in a direction expected from either temperature- or precipitation-based nearest neighbors (Fig. 3). Over half of the species that shifted were subject to opposing directional forces by temperature and precipitation. For these species, movement in one direction potentially represents species-specific sensitivity. Temperature-expected shifts were predominantly upslope (two-sided binomial test, $n = 91$, $p = 0.002$), whereas precipitation-expected shifts tended to be downslope (two-sided binomial test, $n = 94$, $p = 0.079$). Thus, while the direction of climate-induced range shifts may appear 'idiosyncratic,' shift directions were consistent with dual climatic niche factors that are thought to frequently limit range boundaries (Grinnell, 1917; Tingley et al., 2009; Wiens et al., 2010).

Over half of the species in each region were not found to have significantly shifted their elevational range, despite regional climatic expectations to do so (Table S1). Several species traits were strong predictors of range shifts, but not in the direction of a priori expectations. Clutch size and territory type were included in top models for both upper and lower range limit movements (Table 2). Species with small clutches were more likely to shift range than species with large clutches (Fig. 4a), and species holding all-purpose (type A) territories had 3.3 times greater odds of shifting their upper range limits than less territorial species (i.e., non-type
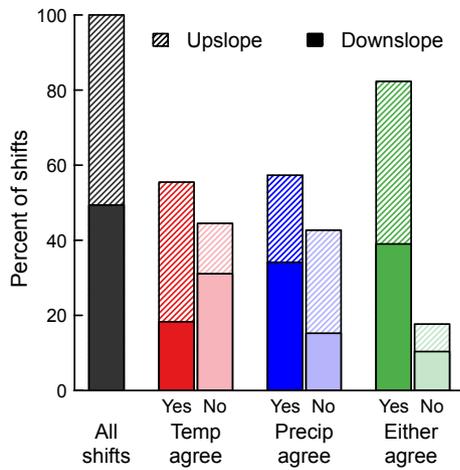
Fig. 3 Agreement between observed elevation shifts and climatic expectations of range shifts derived from modern-temperature and modern-precipitation nearest neighbor elevations. Observed upslope (shaded) and downslope (solid) shifts can be divided into groups that were in agreement with either temperature or precipitation (red bars and blue bars, respectively), or in agreement with either climatic parameter (green bars). Data are aggregated for upper and lower range limits and for all three regions. Not represented are the 302 occasions where a species did not substantially shift a range limit within a region.

A) and 2 times greater odds of shifting their lower range limits (Fig. 4b). There were also differences in the probability of lower-limit range shifts among species depending on their migratory status: short-distance migrants and year-round residents were more likely to shift lower limits than long-distance migrants (Fig. 4c). Finally, upper limit shifts tended to occur more often for dietary specialists, although intramodel support for this trait was marginal (Wald test: $P = 0.13$).

Discussion

We present strong evidence for 20th century elevational shifts in breeding distributions for birds in montane regions of western North America. When viewed in combination with contemporaneous studies of central Sierra Nevadan mammals (Moritz *et al.*, 2008), butterflies (Forister *et al.*, 2010), and vegetation (Crimmins *et al.*, 2011), a clear pattern emerges of how recent climate change has drastically altered the elevational distributions of montane species. Our results highlight, however, that elevational change is not unidirectional; rather, there is substantial variation in the direction and magnitude of elevational shifts both among species and within species among regions. While there is a detectable signal of species shifting up, consistent with a century of average warming temperatures, our results caution that climate change impacts on species' ranges,
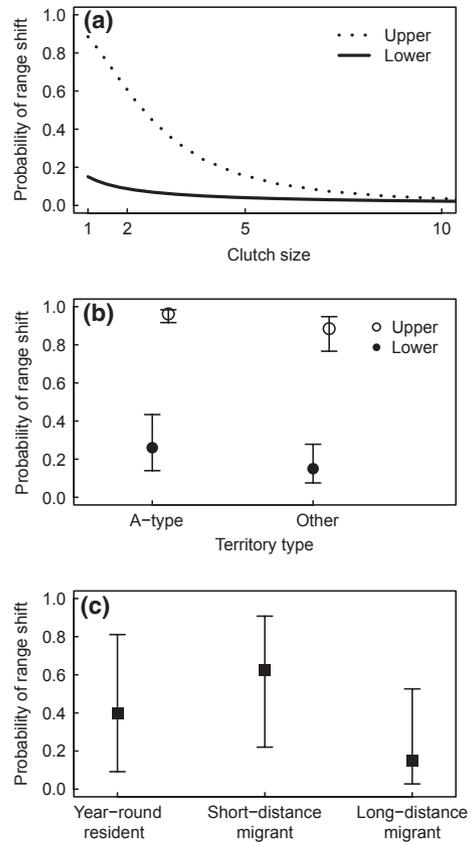
Fig. 4 Relationships between species' traits and the probability of a range shift (regardless of direction). Upper and lower limits were more likely to shift for (a) species with small clutches, and for (b) strongly territorial (A-type) species. Lower limits were significantly more likely to shift for (c) year-round resident species of California, particularly short-distance migrants. Error bars represent 95% confidence intervals around estimated parameter means.

including likely future shifts, are context dependent, with species- and site-specific differences.

Meeting predictions: temperature vs. precipitation

Our results demonstrate that site-specific expectations of the direction of elevational shift, based on both temperature and precipitation changes at a site, were substantially more successful at predicting observed shifts than the uniform hypothesis that all species should shift upslope. Only 51% of significant range shifts pooled across regions and species were upslope. However, 82% of significant range shifts were in accordance with expectations from each species' nearest climatic neighbors based on both temperature and precipitation changes (Fig. 3). Although the northern (Lassen) region barely warmed on average over the last century, showing localized areas of marginal warming and cooling

Table 2 Generalized linear mixed models testing species traits in relation to whether species shifted elevational range limits in any direction

Range limit[*]	Model name[†]	K	$\log \mathcal{L}$	AIC	ΔAIC[‡]	w_i
Lower	migratory status + territoriality + clutch size	5	−100.6	213.1	0.0	0.42
	migratory status + territoriality	4	−101.9	213.7	0.6	0.31
	migratory status	3	−103.4	214.8	1.6	0.19
	migratory status + elevational zone	4	−103.3	216.6	3.5	0.07
Upper	territoriality + clutch size + diet + elevational zone	4	−114.8	241.6	0.0	0.50
	territoriality + clutch Size + elevational zone	3	−115.9	241.8	0.2	0.46

*Species traits were tested separately for each range limit.
†Models were initially built testing species traits individually. Composite models testing multiple traits were *ad hoc* tested subsequently with only those traits that lowered AIC score. For explanations of life history covariates, see Methods.
‡Only models with ΔAIC values less than 4 (indicating strongly supported models) are shown (see Table S5 for all models).

(Fig. 1b), the proportion of bird species shifting there was comparable to the other two regions that experienced substantial warming (Fig. 2). Thus, the northern Sierra Nevada illustrates the failure of the uniform expectation that warming alone will predict range shifts.

The biggest improvement to models of elevational range shift came from incorporating precipitation changes into directional expectations. Precipitation change led to expectations of downward movements that were opposed to most temperature-based expectations of upward shifts. While precipitation explained a greater proportion of shifts, directional shifts on the whole were best explained by both temperature and precipitation together (Table 1, Fig. 3). Thus, the opposing push of rising temperature driving species upslope and the pull of increased precipitation driving species downslope aptly describes the majority of 20th century avian elevational shifts in the Sierra Nevada mountains.

Variability in species' responses to climate

Precipitation and temperature are likely to vary in their magnitude of influence among species and across sites. Generally, ranges of low-elevation species may be more limited by biotic factors (e.g., species interactions), whereas ranges of high-elevation species may be more limited by abiotic factors (Brown *et al.*, 1996). However, using different inferential methods, Tingley *et al.* (2009) found that low-elevation birds in the Sierra Nevada were more likely to shift their occurrence in climate space toward more favorable precipitation conditions, whereas high-elevation species were more likely to shift toward favorable temperature conditions. Consistent with this pattern, using our geographically expanded and more species-rich data set we found that lower limits had directional shifts best described by precipitation, whereas upper limits had directional shifts best described by temperature.

Our results also highlight the importance of local climatic contexts in creating variability in measured elevational shifts. Of the 53 species that we tested for range shifts in all three regions, 11 species shifted range boundaries in opposing directions across two regions. This variation may be explained by species responding to site-specific climate change in each region. For instance, in the Southern Sierra, which is the warmest and the driest region (Fig. 1b), precipitation explained a greater proportion of range limit movements than temperature (Table S1). For five of the 11 species (Fox Sparrow, Hermit Thrush, Bewick's Wren, Bushtit, and House Finch), diverging directional response is explicitly predicted by precipitation, and it is predicted for two additional species (Warbling Vireo and White-breasted Nuthatch) by temperature (Table S1). Grinnell (1917), posited that different factors limit a species' distribution across its geographic range. Modern theory concurs, suggesting that different biotic and abiotic factors can switch from nonlimiting to range limiting quite rapidly, with only small changes in the balance of the factors (Gaston, 2009). Given differing climatic regimes in our three regions and contrasting climate histories over the last century, our results support these theoretical expectations.

To shift or not to shift

Of critical importance to conservation are reasons why species do not shift their ranges given climate change (Dawson *et al.*, 2011). In the Sierra Nevada, 10 of 53 (19%) species analyzed across all three regions did not shift by any metric in any region. Although there are numerous theoretical reasons why species may not shift in response to climatic change, we found that certain species traits were associated with range shifts (Fig. 4). However, these relationships were generally opposed to *a priori* predictions from dispersal-related hypotheses. We found species were more likely to shift their range

if they had smaller clutches, defended all-purpose territories for feeding and breeding, and were year-round residents of California (i.e., short-distant or nonmigratory species).

An alternative hypothesis is that the likelihood of a range shift relates to behavioral plasticity over the life span of an individual. For instance, neotropical migrants have shorter life spans than resident species (Martin, 1995), and clutch size is typically inversely related with longevity (Sæther, 1988; Martin, 1995). Climate change may impact bird ranges through indirect pathways by changing food availability and nest success (Sanz et al., 2003; Both et al., 2006), both of which can impact breeding site fidelity (Greenwood & Harvey, 1982; Hoover, 2003). Long-lived birds have more opportunities to incorporate past knowledge of breeding success into the selection of future nest sites. Moreover, if phenological shifts in food availability are a key proximate cause of differential population declines across a range (Both et al., 2006, 2011), species defending feeding territories might experience greater pressure to search for and defend climatically favorable (and thus food-resource favorable) territories than species that travel great distances in search of food. Our species' trait analysis (Table 2; Fig. 4) suggests that it is not the physical ability to disperse that prevents bird species from shifting their elevational range. Rather, there may be a complex interplay between the differential effects of climate change and phenological shifts on nest-site selection among birds of different life history patterns.

Origins of a heterogeneous response

Our results suggest that a heterogeneous mixture of elevational range shifts for birds of the Sierra Nevada over the past century (Fig. 2) resulted from the combined effects of: (1) temperature pushing species upslope and precipitation pulling them downslope; (2) variation among species in their relative sensitivity to temperature and precipitation; (3) spatial variation in recent climate change; and (4) differing propensities to shift depending on species traits. Our results also demonstrate that site-specific expectations of the direction of elevational shift, based on the climatic history of a site, will be substantially more successful at predicting observed shifts than the naïve expectation of upward movements, and could explain why studies with limited geographical sampling have not always shown such trends (e.g., Archaux, 2004). Our results also highlight the importance of accounting for precipitation in climate-change impact studies, as has recently been demonstrated by Bonebrake & Mastrandrea (2010) for butterflies and Crimmins et al. (2011) for trees. Despite

examples of precipitation having direct impacts on the population growth and survival rates of birds (Sanz, 2002; Schaub et al., 2005; Robinson et al., 2007; Seamans & Gutiérrez, 2007) and other terrestrial vertebrates (King et al., 1991; Frick et al., 2010; Warner et al., 2010), studies of range shifts remain largely within a temperature-centric paradigm.

The failure of most empirical studies of climate-change impacts to include precipitation and other climatic dimensions highlights critical research needs in global change biology. The future of predictive modeling of climate-change impacts may lie in coupling environmental niche-based models of species distributions with mechanistic relationships between environmental suitability and fitness (Kearney & Porter, 2009; Brook et al., 2010). This requires a better understanding of the direct effects of climate change on physiology (Kearney & Porter, 2004), the indirect effects of climate change on habitat change (Crimmins et al., 2011), and the interactions of precipitation and temperature change, for example, through net primary productivity (Tingley et al., 2009). Although the past century has seen increased precipitation throughout much of California and North America, predictions for future precipitation remain highly uncertain (IPCC, 2007). Determining how climatic forces push and pull species in opposition or in agreement requires a more nuanced view of climate change impacts, and holds the key to predicting which species are subject to increasing threats and where species turnover will be greatest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Schematic of how climatic nearest neighbors lead to predictions of elevational shifts.

Appendix S1. Supplementary methods.

Appendix S2. Plots showing detections and nondetections by elevation and survey period for 99 bird species in each of three Sierra Nevadan regions.

Table S1. Observed historical range, significant change in elevational range over time, and predicted change in range based on temperature and precipitation nearest neighbors.

Table S2. Descriptions and parameterizations of 25 occupancy (ψ) models with main, additive and multiplicative effects.

Table S3. Life history and other species characteristics used in traits analysis.

Table S4. Full results of GLMM analysis in explaining the pattern of upslope and downslope movements of 99 bird species in three regions of the Sierra Nevada, California, over the last century.

Table S5. Full results of GLMM analyses for tests of species traits that relate to whether species shifted elevational ranges in any direction.

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