Cryptic loss of montane avian richness and high community turnover over 100 years

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Abstract. Although there are numerous examples of individual species moving up in elevation and poleward in latitude in response to 20th century climate change, how communities have responded is less well understood and requires fully accounting for changes in species-specific detectability over time, which has been neglected in past studies. We use a hierarchical Bayesian occupancy model to examine bird species richness change and turnover along three elevation gradients surveyed 80–100 years apart in the Sierra Nevada of California, USA. Richness declined over the 20th century across all elevations. Turnover was greatest at the highest and the lowest elevations. These findings were only apparent, however, after species' detectability was incorporated into measures of species richness. Further partitioning of species richness changes by elevational life zone showed that numbers of low- and high-elevation species declined, without a concurrent expansion by mid-elevation species. Our results provide empirical evidence for biodiversity loss in protected montane areas during the 20th century and highlight the importance of accounting for detectability in comparisons of species richness over time.

Key words: birds; climate change; detectability; elevational gradient; hierarchical model; resurvey; richness loss; Sierra Nevada, California, USA; turnover.

INTRODUCTION

Assessing change in species diversity is critical to understanding the long-term community-level impacts of climate change. Although there are numerous examples of individual species moving up in elevation and poleward in latitude in response to contemporary climate change (Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011), generalized empirical patterns of climate-induced changes in species richness along elevational or latitudinal gradients are rare (Böhning-Gaese and Lemoine 2004, Pauli et al. 2012). Most studies have examined range shifts of individual species or a priori selected groups of easily detectable species (Chen et al. 2011), thereby inferring changes to total species richness based on an incomplete sampling of the species pool. Projections of future responses for entire communities include putative substantial losses of species diversity (Thomas et al. 2004, Jetz et al. 2007) with climate change posing particular risks to those species endemic to montane regions (Sekercioglu et al. 2008).

Despite long-term predictions of richness loss, evidence for declines in species richness from climate change is equivocal, especially along elevational gradi-ents. Recent studies of climate-change impacts on montane regions have documented species richness declines with elevation (Wilson et al. 2007, Moritz et al. 2008), richness increases with elevation (Grabherr et al. 1994, Popy et al. 2010), and elevation-dependent (Forister et al. 2010) or region-dependent (Pauli et al. 2012) richness changes. The lack of uniform empirical observations on richness may be accurate depictions of taxa- and region-specific differences in response to climate change, but they may also be partially due to sampling artifacts along elevational gradients (Rowe 2005, Rowe and Lidgard 2009). In particular, imperfect detection of species can bias measures of richness and community structure (Kery and Royle 2008, Popy et al. 2010). Since detectability is likely to increase over time due to differences and improvements in survey methods, effort, technology, and knowledge (Tingley and Beis-singer 2009), it is critical that empirical studies of richness change account for detection changes.

This study uses unbiased estimators of species richness that incorporate detectability to explore how bird species richness and turnover have changed in the Sierra Nevada mountains with a century of climate change. Over the last 100 years, minimum and maximum annual temperatures have increased between 1° and 2°C in the Sierra Nevada (Bonfils et al. 2008). Recent research found that temperature and precipitation changes during the last century in the Sierra Nevada have led to range shifts for individual species of birds (Tingley et al. 2012), mammals (Moritz et al. 2008), butterflies

(Forister et al. 2010), and plants (Crimmins et al. 2011); although species often shifted upward in elevation, downward movements were common and much spatial variation exists. Community changes are the cumulative consequence of individual range shifts (Menéndez et al. 2006), and have generally been unanalyzed in past studies. Moreover, analyses have often been restricted to species that were relatively well sampled and it is unclear if these species can be generalized to entire taxon communities. Long-term projections of climate change impacts (Thomas et al. 2004, Jetz et al. 2007) suggest that richness should decrease along elevational gradients, although an extinction debt may lead to temporary increases in richness when the pace of colonizations exceeds extinctions (Walther et al. 2002, Menéndez et al. 2006). In comparison, species turnover is predicted to be greatest at middle elevations (Stralberg et al. 2009), where low-elevation species should shift up and replace mid- to high-elevation species.

While numerous methods have been developed to estimate true richness based on extrapolations from species-abundance or species-accumulation relationships (Chao 1984, Colwell and Coddington 1994), we use occupancy modeling (Dorazio and Royle 2005, Dorazio et al. 2006) in order to preserve species-specific and survey-specific detectability. By modeling species rather than richness, we can quantify both temporal turnover and richness changes at three scales across resurveyed sites: (1) changes in total species richness; (2) changes in richness within elevational groupings of species; and (3) changes in occupancy of each species. This approach allows us to ask multiple questions of how bird communities have changed along an elevational gradient over the past century. Has overall richness increased or decreased? Are richness changes uniform across the elevational gradient? Have species in different elevational life zones changed more than others? Answering these questions across broad regions and over time scales that are relevant to climate change (i.e., decades to centuries) is critical for understanding future impacts of climate change.

Materials and Methods

Study sites and bird surveys

Survey sites were distributed across three elevational cross sections (hereafter "regions") of the Sierra Nevada mountains of California, USA (Tingley et al. 2009, 2012). This area has seen significant anthropogenic-induced climate warming over the last 80 years, especially during the avian breeding season in spring and summer (Bonfils et al. 2008). A total of 77 sites were resurveyed for birds between 2003 and 2009 (Tingley et al. 2012). Sites were historical survey locations that had been repeatedly visited between 1911 and 1929 by Joseph Grinnell and colleagues from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley (see Plate 1). Survey sites ranged in latitude (35.325–40.647° N), longitude (122.219–

118.140° W), and elevation (61–3356 m), and represent the full array of Sierran vegetation-based life zones. Sites were located primarily in protected areas (87%), minimizing potential land use interactions. Although no major land use disturbances were recorded at survey sites, much of the Sierra Nevada region has been subject to fire suppression during the course of the intervening years. In rare instances ($n = 5$) where historical sites were partly or mostly converted to habitats that differed from original conditions or were otherwise inaccessible, proxy sites within 1 km and containing the originally described habitat composition were surveyed instead.

Details of the historical and modern sampling methods are provided in Tingley et al. (2012) and briefly described here. Historical bird surveys followed precursors of line-transect methods. These detection/nondetection surveys were often repeated at daily intervals, with a maximum of 17 visits (median = 3). Surveys listed all species encountered, providing reliable detection/nondetection data. Locations, bird lists, and relevant metadata were extracted from historical field notes archived at the MVZ (*available online*).[4] Modern bird surveys were conducted as part of a systematic multi-taxon resurvey of the work by Grinnell and others (Moritz et al. 2008, Tingley et al. 2009, 2012). Five primary observers conducted point counts following, as best as possible, the same routes taken by historical surveyors, using variable-distance point counts lasting seven minutes. Point count stations were separated by a minimum of 250 m and were placed along the full extent of the historical route (median of 10 points over 2.5 km). Sites were resurveyed repeatedly, often on successive days, with a maximum of five visits (median = 3). All modern occurrence records are archived online in the MVZ's collection database (*available online*).[5]

The analysis of bird survey observations was limited to detections that characterized breeding communities. Historical surveys were conducted between late March–early October, with 87% taking place between May and August. Modern surveys were entirely conducted between May and August. Individual birds from either time period identified as juveniles or in-transit migrants were excluded from analysis to avoid potential bias in the characterization of breeding bird communities. A total of 205 nonmigratory bird species were detected at least once in either time period (172 in historical period, 190 in resurveys).

Occupancy-type studies based on repeated surveys may be susceptible to bias from violations of assumed closure (Rota et al. 2009). These violations are greatest when comparing small sampling units (e.g., individual point counts) rather than large units (e.g., multi-point transects, as characterize our samples); small areas are more likely to intersect only fractions of animal territories (Rota et al. 2009). With respect to the present

[4] http://bscit.berkeley.edu/mvz/volumes.html
[5] http://arctos.database.museum/

study, error from closure, if any, is likely to bias results only if the error was greater in either the historical or modern survey period. To explicitly avoid this, sites in both eras were revisited using a similar temporal sampling structure. Historically, 79% of sites were revisited entirely within one breeding season, and most (66%) were revisited entirely within one week; the remaining sites were surveyed across two or more years. In the modern resurvey, 80% of sites were entirely revisited within one breeding season and 53% were revisited entirely within one week; the remaining sites were surveyed across two years. Similarity of the two sampling schemes suggests that there should be no directional effect of bias from closure violation on inter-era comparisons. Statistical simulations for single-season occupancy models supporting this conclusion are presented in Tingley et al. (2012), as is additional information on the temporal structure of surveys.

Latitude-adjusted elevation

We standardized elevations by latitude to aggregate species sightings across the three regions of the Sierra Nevada into a single elevation gradient. Along mountain ranges oriented primarily in a north–south direction, species in the northern portion have different elevation ranges than in the south (Merriam 1894). The rate at which elevational communities change with latitude is ultimately determined by the rates at which temperature varies with elevation (lapse rate) and with latitude (meriodonal gradient), although estimates for rates can differ by taxon (Cogbill and White 1991) and geographic region (Diaz and Bradley 1997). Brock and Inman (2006) derived latitude-adjusted elevations for the montane western United States based on the change in tree line with latitude, which was estimated to decline 130.1 m per increase of 1° latitude. We used this rate to adjust elevations of all survey sites, standardizing them to the latitude of 35.3° N (the southern-most survey site).

Life zone classifications

Life zone classifications were used as proxies for groupings of species' elevational affinities. We did not assume that species within the same life zone consisted of a single uniform community, or that all species within a life zone behaved uniformly in response to environmental change. Instead, we used elevational life zones to understand changes in richness at an intermediate scale between total richness and individual species, much as elevational and habitat affinities were used to understand how plant communities originally surveyed by Whittaker have shifted along elevational gradients (Harrison et al. 2010).

Species were categorized a priori into life zone groups based on classifications of their predominant historical breeding zone in the Sierra Nevada using Grinnell's monographs (Grinnell and Storer 1924, Grinnell et al. 1930). Grinnell based his life zones on Merriam (1894), with the following groupings, from lowest elevation to highest elevation: Lower Sonoran ($n = 28$ bird species), Upper Sonoran ($n = 53$), Transition ($n = 50$), Canadian ($n = 29$), Hudsonian ($n = 8$), and Alpine/Arctic ($n = 1$). Species that were detected in surveys and not classified by Grinnell were lumped into a single "unclassified" category ($n = 36$). As only one species, *Leucosticte tephrocotis* (Gray-crowned Rosy-Finch), was classified as Alpine, it was lumped with the Hudsonian life zone for analysis.

Multispecies occupancy model estimation of species richness

Multispecies occupancy models (Dorazio and Royle 2005) implement individual species' models of occurrence within a hierarchical (i.e., multilevel) framework. They have been used to estimate total community richness (Dorazio et al. 2006, Kery and Royle 2008) and the effects of different habitats or treatments on richness and community structure (Zipkin et al. 2009, 2010). Although true community properties in nature cannot be known with certainty, these methods produce unbiased results while also accounting for detection heterogeneity (Kery and Royle 2008).

Multispecies hierarchical community models (Dorazio and Royle 2005, Dorazio et al. 2006) draw species-specific occupancy and detectability parameters from hierarchical distributions governed by hyper-parameters with modeled means and variances. By combining all species through the same hierarchical process, inference can be made for species with few detections that otherwise would be difficult or impossible to model on their own (Link and Sauer 1996). Hierarchical models estimate the probability of occupancy of every species without a priori assumptions of how species should co-occur. While relating all species through hyper-parameters can potentially lead to smoothing of regression coefficients, the method draws strength by allowing estimation of community descriptors that depend on having data for all species (Zipkin et al. 2009).

We simultaneously modeled historical and resurveyed sites ($n = 77$ for each) by combining all sites in both time periods ($n = 154$) and fitting "single-season" occupancy models that were allowed to differ by survey era (historical vs. modern) (MacKenzie et al. 2002, Tingley and Beissinger 2009). By allowing occupancy to vary by survey era, the probability of occurrence of a species at a site in the modern time period was modeled independent of its historical occurrence at the same site. This parameterization works well when sampling periods are separated by a sufficiently long time to warrant the assumption of independence (Moritz et al. 2008, Tingley and Beissinger 2009) and when a dynamic model that includes two additional parameters (colonization and extinction) is unable to converge due to data limitations (MacKenzie et al. 2003).

We developed a multispecies hierarchical community model based on survey-specific detection/nondetection records to estimate species-specific occupancy status

and community metrics for each survey era. Observed data, $y_{i,j,k}$, for species $i = 1, 2, \ldots, 205$ at site $j = 1, 2, \ldots, 154$ on survey day $k = 1, 2, \ldots, 17$ were modeled as resulting from the imperfect observation of a true occurrence state, $z_{i,j}$, given a probability of detection, $p_{i,j,k}$. This observation process was modeled as, $y_{i,j,k} \sim$ Bernoulli($p_{i,j,k}z_{i,j}$), where $z_{i,j} = 1$ if species i was truly present at site j, and $z_{i,j} = 0$ if species i was not present at site j. Following Kéry and Royle (2008), the observed data set for $N = 205$ species was augmented by including empty (i.e., all zero) detection histories for an additional $M = 300$ hypothetical, or "unobserved," species (Dorazio et al. 2006). Consequently, the true occurrence state was modeled as $z_{i,j} \sim$ Bernoulli($\psi_{i,j}w_i$), where $\psi_{i,j}$ was the probability of occupancy by species i at site j, and w_i was the probabilistic outcome of a single, zero-inflation parameter, Ω, such that $w_i \sim$ Bernoulli(Ω). For more detail on data augmentation, see Dorazio and Royle (2005), Dorazio et al. (2006), and Royle and Dorazio (2008). Hypothetical species added through data augmentation are not included in results of site-specific estimates of species richness as they lack independent site-specific covariate relationships.

Consistent with single-species approaches to occupancy modeling, probabilities of occupancy and detectability were modeled as linear combinations of site- and survey-specific covariates. Following previous single-species models of birds in this region (Tingley et al. 2012), two covariates were chosen to describe detectability: the historical or modern time period in which the survey was conducted (era) and the linear and quadratic effect of season (jday), as defined by the day of year (i.e., 1 January = 1). Additional detection covariates, such as individual observer effects, increased the complexity of the model without improving the interpretation of outcomes (Tingley et al. 2012). While the historical data did not include a consistent metric for survey effort, we have no evidence that observer-independent effort differences in the historical period would systematically bias detection probabilities upward or downward. The probability of detection was modeled as follows, where $\alpha_{0\ldots3}$, are model coefficients for detectability:

$$\text{logit}(p_{i,j,k}) = \alpha_{0,i} + \alpha_{1,i}\text{era}_j + \alpha_{2,i}\text{jday}_{j,k} + \alpha_{3,i}\text{jday}_{j,k}^2.$$

Expanding on the single-species models used by Moritz et al. (2008), occupancy was modeled as a linear function of survey era (era), the linear and quadratic effect of elevation (elev), and the survey region (defined by two dummy variables, $R1$ and $R2$). Because elevations were adjusted for latitude, it was unnecessary to include interaction effects between elevation and region; however, additive effects allowed species to be more or less likely to occur depending on the survey region. As the change in elevational range over time was an effect of primary interest, interactions were included in the model between elevation and era. Occupancy was modeled as follows, where $\beta_{0\ldots7}$ are species-specific model coefficients for occupancy drawn from modeled hyper-distributions:

$$\begin{aligned}\text{logit}(\psi_{i,j}) = &\, \beta_{0,i} + \beta_{1,i}\text{era}_j + \beta_{2,i}\text{elev}_j + \beta_{3,i}\text{elev}_j^2 \\ &+ \beta_{4,i}\text{era}_j\text{elev}_j + \beta_{5,i}\text{era}_j\text{elev}_j^2 + \beta_{6,i}R1_j \\ &+ \beta_{7,i}R2_j.\end{aligned}$$

Continuous covariates (elev and jday) were centered and normalized to a standard deviation of 1 prior to analysis. Each observed species was fit to the four detection parameters and eight occupancy parameters.

Derived community estimates

Parameters that are functions of primary modeled variables can be easily calculated from posterior draws of Markov chain Monte Carlo (MCMC) runs, incorporating estimation error into functions of parameters. We specified several community measures in the model that are direct functions of estimated parameters. Species richness was simply estimated as

$$N_j = \sum_{i=1}^{205} z_{i,j}$$

where N_j is the total number of species occurring at a site in a particular survey era. Richness was further broken down into the components of richness at each site originating from species in different life zones, such that

$$N_{j,\lambda} = \sum_{i=1}^{205} z_{i,j}\lambda_i$$

where the site-specific richness for a given life zone, $N_{j,\lambda}$, is a function of the species estimated to be present ($z_{i,j}$) and whether each species was a member of the life zone (λ_i). We also calculated the total proportion of occupied sites for each species in each time period, historical or modern (ψ_h or ψ_m).

Turnover in the avian community over time at a site was calculated using 1 minus the Sørensen similarity index (Sørensen 1957). Thus, for a historically visited site designated c_a and its modern paired revisit, designated site c_b, turnover, T, between the two bird communities would be calculated as

$$T_c = 1 - \frac{2\sum_{i=1}^{205} z_{i,j=c_a}z_{i,j=c_b}}{N_{j=c_a} + N_{j=c_b}}$$

for sites $c = 1, 2, \ldots, 77$.

Model specification

Bayesian parameter estimation was run with the freely available software WinBUGS (Lunn et al. 2000) via R (version 2.14; R Development Core Team 2011) using the package "R2WinBUGS" (Sturtz et al. 2005). Uninformative priors were used for means and variances of the hyper-parameters. The full model specification is provided in the Supplement. We ran three parallel
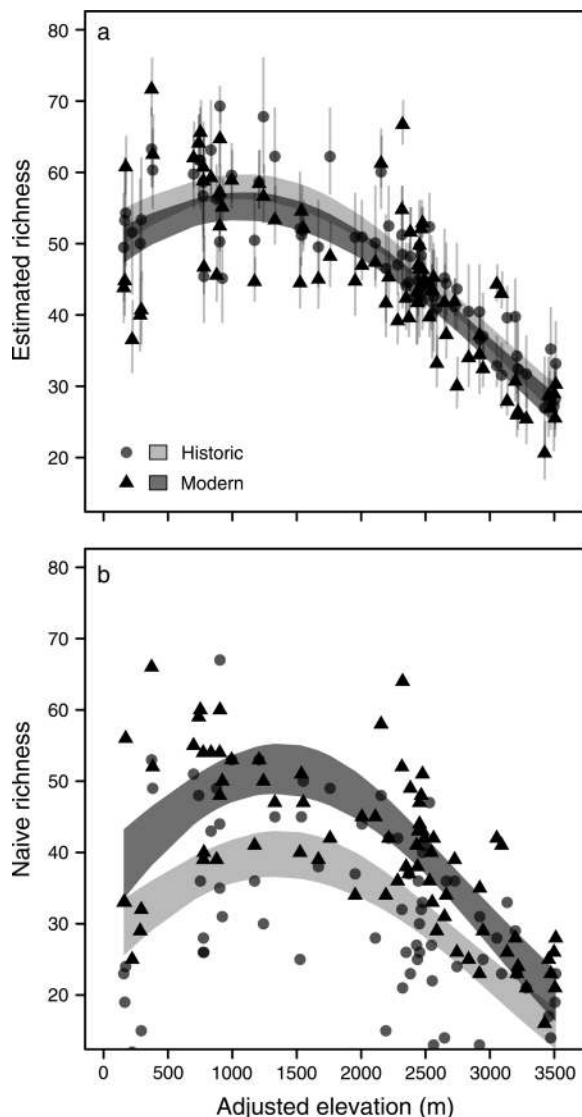
FIG. 1. Patterns of species richness (a) after accounting for nondetected species at each site and (b) based on naive estimates derived solely from detected species. Richness is the actual number of species. Each survey point is represented by its historical richness (circles) and modern richness (triangles). For estimated true richness (a), lines through points represent 95% credible intervals of the posterior distribution. Elevational trends for historical (light gray) and modern (dark gray) richness are depicted by 95% confidence intervals around predicted relationships derived from linear regression of posterior means of site richness (a) and observed site richness (b). Site elevations are adjusted to account for latitudinal effects.

chains of length 50 000, discarding the first 40 000 as burn-in, and used a thinning rate of 10. This resulted in a posterior distribution consisting of 3000 samples for each parameter. Convergence was assessed by visual inspection of traceplots and by using the Gelman-Rubin convergence diagnostic (Gelman et al. 2004) with all diagnostic values <1.1. Posterior occupancy parameter

means for all species are included in Table A1 in the Appendix.

Testing hypothetical models of richness change

Richness for all species and for species in each life zone was tested for change over time with respect to the elevational gradient. For each species assemblage, the mean posterior richness for each site was modeled using a general linear model with a log-link and Gaussian error distribution. Each regression was weighted by the posterior variance of richness estimates. Eight models of richness patterns (i.e., the full set of models involving elevation, elevation^2, and era) were tested for each species assemblage, with the best model selected through the minimization of Akaike Information Criterion (AIC) scores (Burnham and Anderson 2002). A list of all models tested for each species assemblage as well as AIC scores are presented in Table A2 in the Appendix.

RESULTS

Changes in species richness over 100 years

Bird species richness decreased across the full elevational gradient in the Sierra Nevada over the 21st century when we accounted for unobserved species at sites (Fig. 1a). Modern species richness was significantly less than historical richness (i.e., 95% credible intervals of richness differences nonoverlapping with 0) at 21 sites (27%), while only seven sites (9%) gained a significant number of species. More generally, using mean posterior estimates of richness change, significantly more sites lost species than gained species (57% vs. 43%; χ^2 test, $P = 0.007$). Sites with significantly lower richness (based on 95% credible intervals) were dispersed across the entire elevational gradient, but a greater proportion of sites had significantly lower richness at the highest and lowest elevations (Appendix: Fig. A1). Significant declines in estimated richness ranged from 4.6 to 15.0 species per site (median of all sites = 2.6 species lost).

General linear models tested whether the richness curve changed over time using posterior means of site richness as a function of elevation and era (Appendix: Table A2). In the best-supported model, richness had a quadratic relationship with elevation, with a peak richness at 994 m (elevational equivalent at 35° N), which was constant through time (Fig. 1a). Across all elevations, richness decreased by an average of 2.5 species per site over the 21st century.

Consequences of imperfect detectability

Imperfect detection of species biased the interpretation of richness change. Detectability varied widely by species and in relation to different factors (Appendix: Fig. A2). Species' detectability generally increased at the peak of the breeding season with declines on either side. There was a moderate correlation between average detectability and occupancy ($\rho = 0.48$), suggesting a potential effect of abundance on detectability, but this value is lower than for other similar studies (Zipkin et al.

2009). Detectability appeared to be a strongly species-specific trait with high variation even within taxonomic families. Critical to the interpretation of richness change, the mean probability of detection differed markedly between historical and modern surveys (Appendix: Fig. A2a). For a single survey at a site in the middle of the breeding season, the mean probability of detection for a species at historical sites was 0.37 (95% CI: 0.35–0.39), while at modern sites it was 0.62 (95% CI: 0.59–0.64). On a species-by-species basis, detectability per site per visit was significantly greater in modern surveys than historical ones (paired *t* test: $t_{204} = -29.8$, $P < 0.001$).

Differences in detectability over time led to differing counts of per-site species richness based on observed species vs. estimated true richness (Fig. 1). After accounting for undetected species, richness of the average historical site increased by 16.9 species, while richness of the average modern site increased by 5.1 species. This difference led directly to divergent interpretations of richness trends over time. The substantial difference in interpretation is particularly clear at the scale of the individual survey site (Appendix: Fig. A1).

Turnover and richness change by elevational life zone

While richness broadly decreased by two species per site, species turnover indicated that an even greater number of species became locally extinct at sites and were replaced by colonizing species (Fig. 2). Community turnover at sites over time ranged between 20% and 49% (median = 35%). Along the elevational gradient, temporal turnover showed a quadratic form with greatest turnover at the extremes of the elevational gradient (Fig. 2).

These same elevational extremes (Lower Sonoran, Canadian, and Hudsonian life zones) showed significant changes in estimated species richness over the last 100 years, while the middle two life zones (Upper Sonoran and Transition) experienced little change (Fig. 3). A linear model of Lower Sonoran species richness indicated that richness significantly decreased over time at low elevations (Fig. 3a). Canadian zone species richness showed significant declines across the gradient (Fig. 3d), with an average loss of 1.4 species per site over time. Similarly, 83% of sites had fewer Hudsonian species estimated in the modern surveys, with the greatest departures at high elevations (Fig. 3e).

Species unclassified into life zones by Grinnell showed a different pattern from the classified species and were estimated to have increased over time at 61% of sites. These sites were distributed across the entire elevational gradient, but unclassified species richness increased most dramatically at low elevations (Fig. 3f). Unclassified species (see Appendix: Table A1 for species list) included species that breed in or near the Sierra Nevada but which are confined to specific habitats (e.g., waterbirds). Unclassified species were not unique to modern sur-
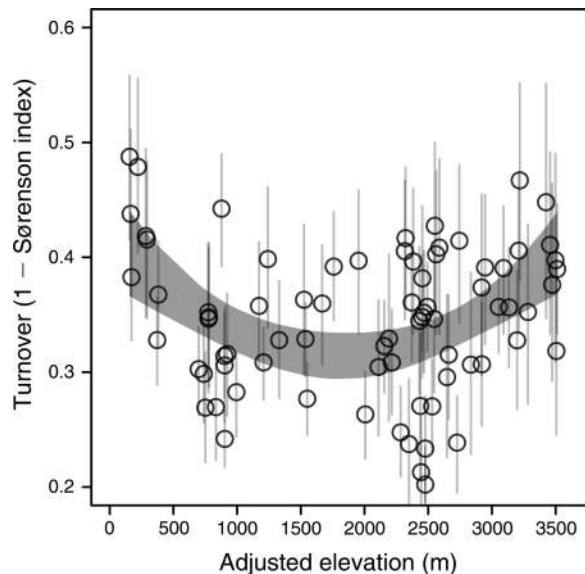

FIG. 2. Occupancy-estimated turnover in species communities at each site between historical and modern surveys. Vertical bars show 95% credible intervals for site-level turnover estimates. Trends line shows 95% confidence interval of the linear regression trend of turnover with elevation. Turnover had a quadratic relationship with elevation, with highest turnover at elevational extremes.

veys; 39% of unclassified species were detected in at least one survey historically.

Species-specific contributions to richness change

Within each life zone, individual species contributed differently to changes in richness, with species having divergent patterns of average occupancy over time (Fig. 4; Appendix: Table A3). The ratio of species' modern occupancy to historical occupancy (Fig. 4) evaluates whether a species has increased (>1) or decreased (<1) across all sites. While the number of increasing species (*n* = 98) was nearly identical to the number of decreasing species (*n* = 107), there were nearly twice as many decreasing species (*n* = 40) with occupancy ratios significantly different from 1 than there were increasing species (*n* = 21). In other words, changes in occupancy were generally larger for decreasing species than for increasing species.

Species with large occupancy changes did not exhibit obvious taxonomic or life history affinities. The 21 increasing species were distributed across 17 avian families, with no family accounting for more than two species. The 40 decreasing species came from 25 families, with Parulidae (four of 11 species) and Turdidae (three of six species) represented most frequently. While many of the increasing species have synanthropic affinities (e.g., American Robin, Mourning Dove, European Starling), this classification only accounted for eight of the 21 increasing species. Controlling for phylogeny, neither clutch size, nesting location, or foraging location
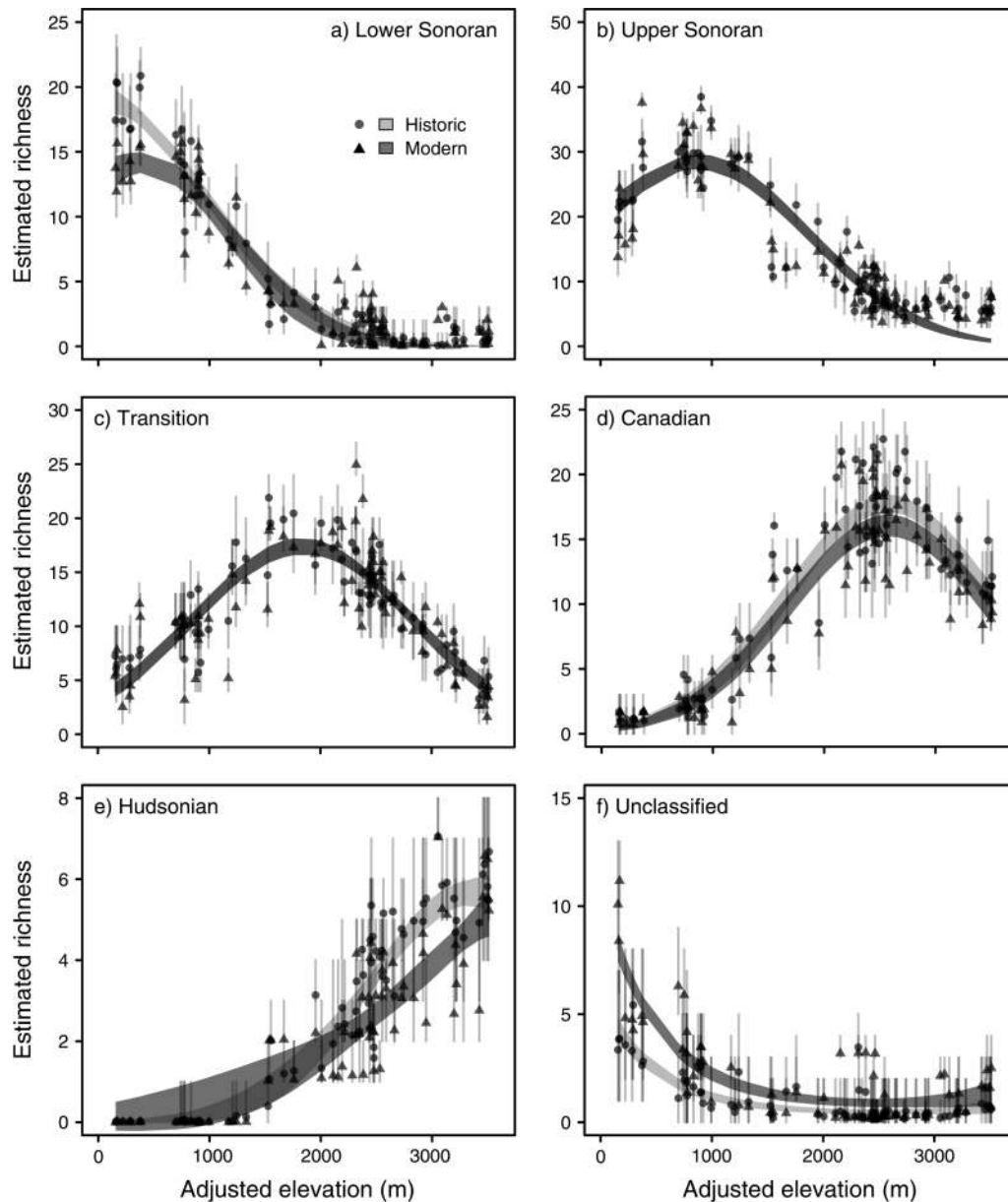
FIG. 3. Difference in per-point richness for species of different life zones in the historical (circles) and modern (triangles) surveys, based on occupancy model results (uncertainty at points shown by 95% credible interval lines). Elevational trend lines for each life zone were estimated using general linear models and are depicted as 95% confidence intervals of the trend with elevation for historical richness (light gray line) and modern richness (dark gray line). Species life zones (a–e, in increasing elevational order) are as labeled.

explained patterns of occupancy change using generalized linear mixed models (Appendix: Table A4).

DISCUSSION

Bird communities along an elevational gradient in the Sierra Nevada showed a large degree of change over the last century. Per-site species richness significantly declined over time; the average site lost only two species, but some sites lost up to 15 species. While the loss of two species may appear small relative to average richness at a

site ($n = 46$), sites experienced an average turnover of 35% of their species pool, indicating a high degree of underlying change in Sierra Nevada bird species composition. Failure to account for species-specific and survey-specific differences in detection led to critically different conclusions about community change.

Elevational patterns in community change

Many taxa show humped or declining patterns of species richness along elevational gradients (Rahbek
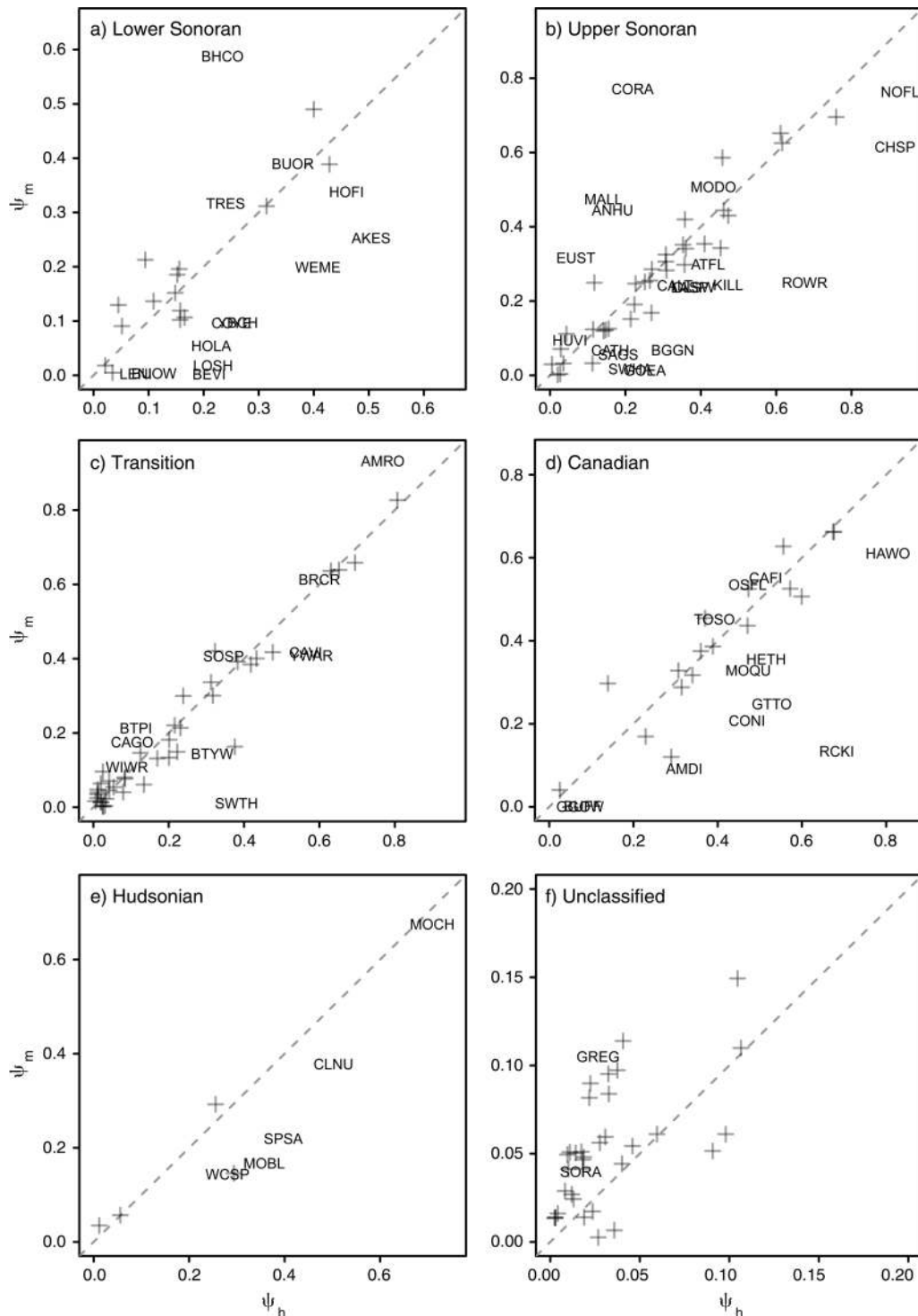
FIG. 4. Individual species' average historical (ψ_h) and modern (ψ_m) occurrence, grouped by elevational life zone. Species above the one-to-one line (dashed) have greater average modern occurrence (i.e., "increasing"), while species below have greater average historical occurrence (i.e., "decreasing"). Only species with modern-to-historical ratios significantly different from 1 are named; all other species are unnamed (crosses). Species on the one-to-one line may show turnover at sites but lack net changes in occurrence. Species life zones (a–e, in increasing elevational order) are as labeled. Key to four-letter species codes and full numerical results are contained in Table A3 in the Appendix.
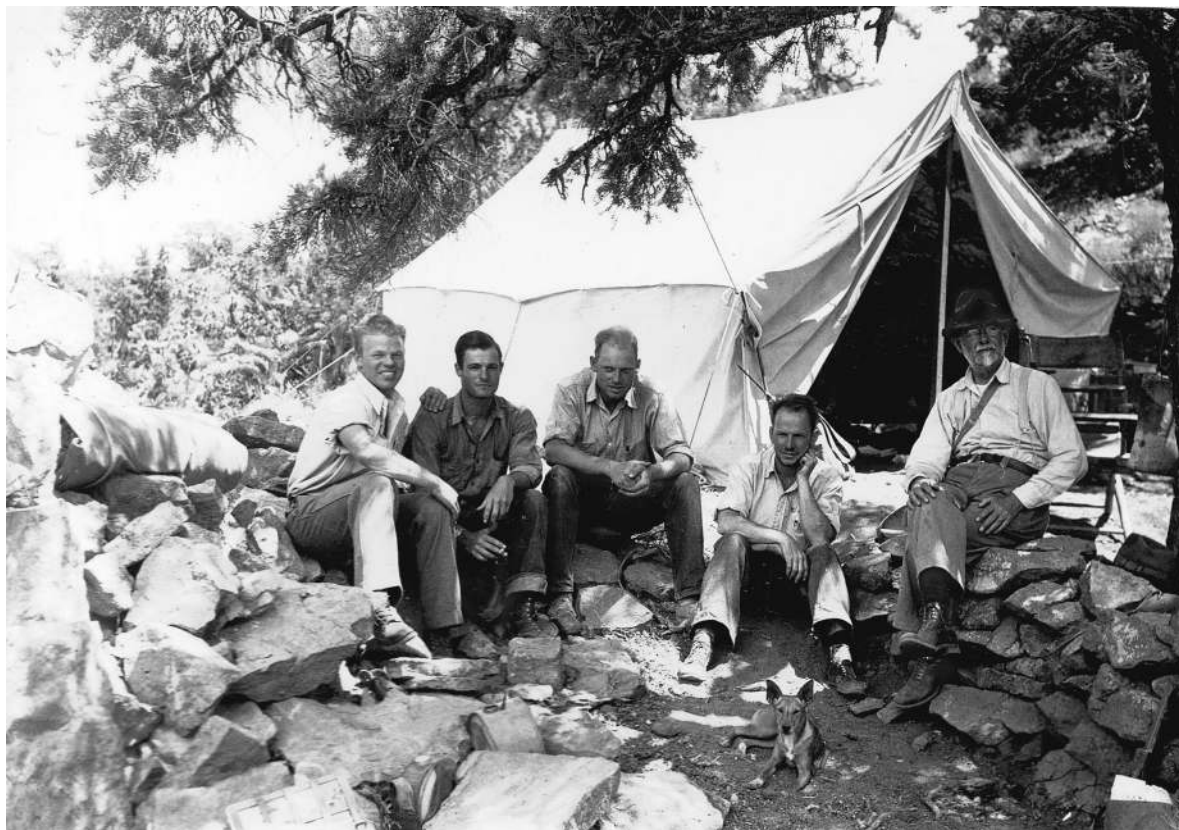
PLATE 1.   Joseph Grinnell (far right) in camp with Museum of Vertebrate Zoology researchers (from right: Elmer Aldrich, Dale Avery, Dave Johnson, and Tom Rodgers), at Cedar Canyon, Providence Mountains (San Bernadino County, California, USA), 1 June 1938. The photo is used with the permission of The Museum of Vertebrate Zoology, University of California, Berkeley.

1997, Grytnes and Vetaas 2002, Sanders 2002, McCain 2009). While we found that bird richness followed a quadratic or humped pattern, maximum richness was near the bottom of the elevation gradient (Fig. 1). There was no statistical evidence that the form of the richness curve changed over time, as can happen when low-elevation areas experience greater land use change and modification than high elevation areas (Nogués-Bravo et al. 2008). Nor was there evidence of a modal shift of the richness curve, which would be expected if communities shifted together upslope (Wilson et al. 2007). Rather, richness decreased equally across the entire elevational gradient.

Turnover in bird species composition in the Sierra Nevada over the past 100 years showed an unexpected relationship with elevation. Based on model projections (Stralberg et al. 2009), the greatest turnover was expected at middle elevations where species shifting upward with climate warming were expected to replace each other. Surprisingly, turnover in our study area was greatest at the lowest and highest elevations (Fig. 2). The potential reasons for this pattern can be explained by examining the richness changes of birds in each life zone individually (Fig. 3). Low elevation areas (<1000 m) experienced a decline in Lower Sonoran species (the

group arguably the best adapted to natural habitats in those areas) and a corresponding increase in unclassified species, which may have taken advantage of the human-modified landscape. High elevation areas (>2500 m) appeared to lose species, with declines in both Canadian and Hudsonian zone species. Richness of middle elevation zone species (Upper Sonoran and Transition) showed no significant changes over time. Thus, the richness component lost from high elevation species was not replaced by upward shifts of mid-elevation species.

Our results agree with previous work showing broadscale declines in richness over time (Wilson et al. 2007), yet they demonstrate that richness shifts result from a high degree of underlying community dynamics. The failure to detect significant changes to the form of the richness curve over time suggests that if bird communities are shifting from climate change, then they are not doing so in unison. Previous work on birds in the Sierra Nevada strongly supports this hypothesis, showing that species individualistically tracked different climatic parameters through time (Tingley et al. 2009, 2012). Additionally, downslope range shifts with climate change can be expected due to spatial variation in both precipitation and temperature change during the 20th century (Tingley et al. 2012), which may explain our

unexpected result of species loss at the highest elevations. Even within the same life zone elevational band, species showed variability in occurrence patterns (Fig. 4), indicating species-specific sensitivities to environmental drivers. A net decline in species richness suggests that these individualistic range shifts have cumulatively resulted in range contractions more often than range expansions (i.e., more site-level extinctions than colonizations). This finding is in contrast to continental-scale studies of latitudinal shifts in North America, that suggest that range expansions may be more common than range contractions (La Sorte 2006, La Sorte and Thompson 2007).

Causes of change in species richness

The attribution of long-term community change through the analysis of occurrence data is hindered by a number of factors. Foremost among these is the differentiation between observed rates of community change over time and the "natural" background temporal variability in the community (Magurran et al. 2010). Bird communities vary from year to year, responding to changes in weather and food resources (Holmes et al. 1986). Additionally, richness is related to the size of the area surveyed (Rahbek 1997) and survey effort (Magurran et al. 2010). Consequently, comparing single snapshots of communities, even within a year, can result in high estimates of turnover (Maron et al. 2005).

Our results are robust to these potential biases. Foremost, our results are derived from repeated sampling both within a year, and in limited cases, across years. Observed heterogeneity in species occurrence within sites and among sites was incorporated into modeled detectability, reducing the potential bias of effort. By accounting for detectability, a very different picture of richness change over time was found (Fig. 1; Appendix: Fig. A1).

Many factors can result in changes to community composition. Habitats can differ in their rates of background turnover (Magurran et al. 2010) and the observed relationship of turnover with elevation may be affected by the change in habitat as elevation increases. Additionally, land use change and vegetation shifts are likely to cause avian species turnover and richness shifts (Yahner 1997, Boulinier et al. 2001). In the Sierra Nevada, land use change has occurred mostly at low elevations (Forister et al. 2010), similar to global patterns (Nogués-Bravo et al. 2008), while the majority of moderate and high elevation areas are protected as state or federal lands. This may very well explain the increase in unclassified species at low elevations; many of these species, including waterbirds, may be responding to increased land use change at low elevations. Additionally, forest composition at all elevations has changed in the Sierra Nevada over the last century (Crimmins et al. 2011), likely due to combinations of climate, disturbance, fire suppression, and succession, with the most prominent change being a decline in *Pinus*

ponderosa (Thorne et al. 2008). This tree species is most characteristic of the Transition life zone (Hall and Grinnell 1919), which, however, exhibited a stable bird community over time (Fig. 3c). Declines in Lower Sonoran (low elevation) and Canadian and Hudsonian (high elevation) species, consequently, are most parsimonious with the individualistic upslope and downslope shifts of species responding to multiple climatic gradients (Tingley et al. 2009, 2012). While no study is likely to show full attribution of results to climate change, the decline in species richness and high turnover are at least partly attributable to shifting patterns of climate in the Sierra Nevada in the 20th century.

Impact of imperfect detection on findings

Differences in detectability over time can have a major confounding effect on revisitation studies of species occurrence. In this study, detectability of bird species substantially increased over a century coincident with changes in survey methodology and dissemination of field-based ornithological knowledge. Analyses accounting for detectability demonstrated a decrease in species richness, while those that did not indicated an increase in richness over time. While the difference in detectability observed over time in this study may be substantial due to the nature of historical survey data, there is strong evidence that surveyors benefit from experience (Sauer et al. 1994) and are biased by previous species encounters at a site (Riddle et al. 2010). Consequently, even surveys conducted by the same observer five or 10 years apart are not immune from temporal changes in detectability.

For these reasons, studies of community properties should account for imperfect detection and allow detection probabilities to vary by species, survey, and over time. To date, no other studies of climate change impacts on species richness have done so. Trends from observed data showing richness declines, even when nonparametric richness estimators are used (Moritz et al. 2008), may be more severe than previously estimated. Additionally, observed richness increases may obscure true decreases. Hierarchical community occupancy models (Dorazio and Royle 2005, Dorazio et al. 2006) provide a strong, flexible framework within which to estimate the processes which obscure true occupancy. Continuing to advance methods of accounting for detectability will be critical for conservation as we use ever more diverse baseline sources of data to understand temporal changes in the natural world.

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SUPPLEMENTAL MATERIAL

Appendix

Additional analyses and species-specific detectability and occupancy estimates (*Ecological Archives* E094-052-A1).

Supplement

BUGS-language model specification of hierarchical community occupancy model (*Ecological Archives* E094-052-S1).