Title

Long-term trends in the avifauna of the Sierra Nevada: community dynamics and species occupancy over a century of climate change

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Publication Date

2011

Long-term trends in the avifauna of the Sierra Nevada: community dynamics and species occupancy over a century of climate change

By

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A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

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Professor Steven R. Beissinger, Chair
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Spring 2011

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Abstract

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Climate change is widely considered to be one of the most important and omnipresent threats to global environmental health and biodiversity. Responding to changing climates, species are expected to shift their geographic distributions in order to remain in physiologically and ecologically favorable climates. These shifts may be species-specific, and different responses of species to a rapidly changing climate have unknown consequences for biotic communities. Despite recent evidence of shifts in mammals and plants, evidence for major changes in the distributions of birds in response to climate change is sorely lacking. Additionally, our understanding of the ecological patterns in which range shifts occur is rudimentary. This is particularly true of montane regions, where there is no clear picture yet as to how animals respond to warming along elevational gradients.

To investigate this subject, I, along with the Grinnell Resurvey Project at the Museum of Vertebrate Zoology (MVZ), resurveyed birds at 95 sites in the Sierra Nevada mountains of California. These sites were originally visited 80-100 years ago by Joseph Grinnell and colleagues from MVZ. The sites were distributed among three primary elevational transects, each extending from near sea level in the Central Valley to the highest peaks of the Sierra Nevada. Comparisons of bird species assemblages at sites across time allowed unique inference on the long-term changes to species' ranges and community composition in California's montane regions.

Our knowledge of current and recent climate-induced impacts have lagged behind predictive work due in part to the difficulties inherent in studying changes over time, requiring both reliable historical data and a robust method to compare these data to contemporary observations. Resurvey studies, where sites with historical species lists are revisited, often after many decades, are critical tools in understanding distributional changes over time. As we show in my first chapter, resurvey studies are increasingly used in ecology to infer extinction, colonization, and range shifts, yet most authors struggle with or completely ignore the problems arising from comparing occurrence data collected by different observers using different methods, sometimes even in different locations. A modeling technique known as occupancy modeling provides a flexible framework by which range shifts can be estimated while accounting for the diverse problems associated with historical data, particularly detectability. In subsequent chapters, occupancy modeling is the key analytical tool I employ permitting robust comparisons of occurrence data across time.

Given climate change, any particular species is expected to shift in geographical space in order to track, or remain within, its favorable niche in climate space. Using occurrence data for 53 western US birds from all resurveyed sites, my second chapter investigates whether documented occurrence changes over the 20th century provide evidence in support of niche tracking. Based on movement directions of occurrence in climate space, we found evidence of climatic niche tracking for 91% of species, with some species tracking only temperature and some tracking only precipitation. Additionally, there was a strong relationship between the environmental factors limiting species' ranges on a continental scale, and the factors tracked over time. Two-season occupancy models further demonstrated that extinction and colonization probabilities for a species were most strongly related to the climatic relationship between a site and the species' niche centroid.

Evidence that species are tracking their climatic niche does not, per se, describe how species are moving in geographic space. Using a larger sample of 99 bird species, my third chapter catalogues the elevational movements of species over time and seeks to test the naïve hypothesis that all species will shift upward in elevation in order to track a warming climate. While species did, on the whole, shift up more than they shifted down, this naïve hypothesis only described 56% of measured range shifts. Alternative hypotheses providing species specific predictions of upward or downward shifts based on site-specific climate change almost universally outperformed the naïve hypothesis. Many species did not shift in parts or all of their range, despite climatic expectations to do so, and traits defining these species and differentiating them from moving species are explored.

The cumulative effect of hundreds of species shifting geographic ranges in an individualistic manner has an unknown effect on local species diversity. My fourth chapter uses a hierarchical multi-species occupancy model to estimate richness change and turnover at sites based on all 210 observed breeding bird species in the Sierra Nevada. The results illustrate that richness has broadly declined across all elevations, but that turnover has been greatest at the lowest and the highest elevations. The results also demonstrate the importance of accounting for detectability using methods such as occupancy modeling, as analyses of community change using naïve detections of species show opposite trends than those inferred when accounting for false absences.

Overall, my dissertation provides a detailed picture, over a uniquely long time span and broad geographic area, of how bird species have responded spatially to changing climates over a century. These movements have been shown to be more diverse than previously described and are not likely to be predicted by simple ecological relationships. As we prepare for greater climate shifts during the 21st century, recovering and utilizing our knowledge of the past will be critical to anticipating and understanding the impacts of the future.

To my parents, Marcia and Tyler, and to my husband, Phil

> "At this point we wish to emphasize what we believe will ultimately prove to be the greatest purpose of our museum. This value will not however, be realized until the lapse of many years, possibly a century, assuming that our material is safely preserved. And this is that the student of the future will have access to the original record of faunal conditions in California and the west, where-ever we now work."
>
> (Joseph Grinnell, 1910)

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Acknowledgements

I am very grateful to the many people who have provided guidance, assistance, and support throughout my experience at Berkeley. Foremost, I am grateful for having had the opportunity to work at Berkeley with my graduate advisor, Steven Beissinger. Steve exemplifies the very best kind of hands-on mentorship. I was continually challenged and encouraged to push my thoughts, ideas, and analyses to higher levels, and I am thankful for his dedication to and endless support for me and my ideas, wherever I was geographically. I am also indebted to Craig Moritz, who has valiantly led the Grinnell Resurvey Project through the best, and the most quagmire-like, of times. I could not have achieved even part of my dissertation work without Craig's foresight and facilitation. I thank Justin Brashares for his honest and caring direction and for being an inspiring role-model. My final committee member, Rauri Bowie, strongly supported my training as an ornithologist and I thank him for his guidance. To two additional members of my orals committee, I thank Claire Kremen for her wisdom and acting as a teaching role-model, and I thank Perry de Valpine for gently nurturing the inner quantitative ecologist in all of us.

My research would not have been possible without the assistance of all those who worked and continue working on the Grinnell Resurvey Project. We are all indebted to the foundational work of Joseph Grinnell, whose legacy we strive to honor. My dissertation greatly benefited by the pioneering resurvey work by Andrew Rush, who collected all the bird observation data from Yosemite and shared these with me. John Perrine, Karen Rowe, and Kevin Rowe all provided invaluable insight and assistance in the logistics of field work, including permissions and access. Michelle Koo continually supplied GIS support and pleasantly tolerated my pestering. I thank Carla Cicero, Chris Conroy and Jim Patton for sharing wisdom gained from their extensive experience in field zoology. William Monahan directly contributed to the development of the ideas presented in Chapter 2. I am additionally thankful for insights provided by Pete Epanchin, Toni Lyn Morelli, Juan Parra, Emily Rubidge, Maria Santos and Adam Smith.

I have had the pleasure of working with many wonderful people during field work. The collection of an astounding quantity of survey data could not have been accomplished in four years without the help of lead surveyors Allison Shultz and Teresa Feo, who also kept me organized, sane, and alive. I am no less grateful to Pascal Title, Paul Newsam, Nadje Najar, Dan Wait, Felix Ratcliffe, Andrew Green, Lacey Hughey, Karen Rowe, and Sara Weinstein, all who helped in data collection and the aforementioned duties (organized, sane, alive). At the Museum of Vertebrate Zoology, Monica Albe provided key support for field preparations, and Stephen Long and Anna Ippolito helped coordinate my time away. I thank the various National Park and Forest Service staff, particularly Jon Arnold at Lassen Volcanic NP, who facilitated access to survey and camp sites. In the Kern River Valley, I am indebted to Reed Tollefson for unfettered access to Audubon Kern River Preserve lands and to Ali Sheehey for her immense generosity and motherly care while staying at her home.

I am thankful for the assorted assistance given to me during the writing and analysis phase of this dissertation. The Beissinger lab, including Philippe Gerard, Laurie Hall, Patrick Kelly, Allison Moody, Orien Richmond, Ben Risk, Matt Shawkey, Erica Spotswood, Corey Tarwater, Sophie Veran, and Jennifer Wang, played an instrumental role in the development of my ideas and analyses. At various points I sought and gratefully received analytical help and

advice on occupancy modeling from Jim Nichols, Jim Hines, Andy Royle, Viviana Ruiz-Guitierrez, Marc Kéry, and Darryl MacKenzie. Terry Root and Kim Hall provided an outside perspective and mentorship through the BICCCA program. I am additionally grateful to Joel Cracraft and George Barrowclough for generously providing an academic home while writing in New York at the American Museum of Natural History. Prior to publication, Chapter 1 benefited from helpful comments by Kevin Winker and three anonymous reviewers, and Chapter 2 benefited from comments by three anonymous reviewers.

I very much appreciate the funding that has supported me throughout my dissertation, including the National Science Foundation, the Department of Environmental Science, Policy and Management, the Museum of Vertebrate Zoology, the National Park Service, and the A. Starker Leopold Chair Fund.

Finally, I thank my family and friends that have supported me throughout graduate school. The terrific friends I made at Berkeley, including Chris, Karl, Luke, and Nick, provided encouragement through the hardest of times. My parents, Marcia and Tyler, have always allowed me to freely pursue my passion wherever it took me and instilled in me the value of a lifetime of learning. Lastly, I thank my husband, Phil, for everything from advice on obscure statistical challenges and feedback on writing to love and support, whether close by or far away.

Chapter 1.

Detecting range shifts from historical species occurrences: new perspectives on old data

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Tingley, M. W., and S. R. Beissinger. 2009. Detecting range shifts from historical species occurrences: new perspectives on old data. Trends in Ecology and Evolution 24(11): 625-633.

Abstract

An obstacle to documenting range change in relation to environmental modifications is making valid comparisons between historical and contemporary data. Recent statistical advances use occupancy modeling to simultaneously estimate both the probability of detection and the probability of occupancy, and enable unbiased comparisons between historical and modern data, but require repeated surveys at the same locations within a time period. Here, we present two models for explicitly comparing occupancy between historical and modern eras, and discuss methods to measure range change. Keepers of historical data have crucial roles in curation and aiding accessibility, while collectors of contemporary specimen data should organize their sampling efforts to include repeated surveys to estimate detection probabilities.

Historical occurrence data: a new opportunity

Documenting range shifts is an integral part of understanding how species and communities have responded to past environmental change and might respond to future environmental modifications (Parmesan and Yohe 2003, Root et al. 2003). A key strategy to documenting range shifts is the use and resurvey of historical occurrence data, such as those from museum collections and field notes (Shaffer et al. 1998). Here, we define historical occurrence data as any set of information that, through observed detections or non-detections, provides evidence on the true presence or absence of individuals of a species (see Box 1). A major obstacle to documenting range change, however, is making valid comparisons between historical and contemporary data (Skelly et al. 2003). Historical species occurrences are often perceived as untrustworthy, and many rich sources of baseline data have been forgotten, lost, or discarded (e.g., Matthews and Heath 2008, Thorne et al. 2008). Compared with contemporary data, most historical data were collected using outdated or different methodologies with associated uncertainties and inaccuracies (Shoo et al. 2006) and might not provide strong inference on change when compared naïvely with modern observations. The rapid pace of environmental change, however, necessitates an urgent reexamination of all potential sources of information on range shifts (Sparks 2007).

Here we describe the types of ecological inference that can be gained from using historical species occurrence data, and the problems associated with making such inferences. Additionally, there have been numerous recent advances in the estimation and statistical modeling of uncertainty, which now enable unbiased comparisons between historical and modern data. By minimizing or controlling for many of the problems that have plagued earlier analyses of historical occurrence data, these techniques can aid in understanding range changes that have already occurred. We hope that future studies will "rediscover" historical occurrence data and provide greater inference on how communities, populations and species have shifted over long temporal scales.

Problems with using historical occurrence data to document range shifts

Variation in the details recorded and methodological characteristics of historical occurrence data largely determine both the problems faced in inferring range change and the solutions available. Here, we group historical occurrence data into four general forms, each differing in the information contained in the data and the resulting inferences available (Table 1). The simplest form of occurrence data is presence-only data, which are widely available from natural history museum (NHM) collections, are used frequently in modeling distributions and are likely to be the most abundant type of historical occurrence data (Graham et al. 2004, Lütolf et al. 2006, Pearce and Boyce 2006). Yet, presence-only data pose several problems for determining changes to species ranges due to their lack of information on non-detections (Zaniewski et al. 2002) (See Glossary). Lack of historical non-detections restricts comparisons with modern data to only those locations where species once occurred, enabling an estimate of extinction (or its converse, persistence) but not colonization (Parsons et al. 2008). The use of randomly generated "pseudo-absence" data sets has become popular in modeling distributions from presence-only data (Lütolf et al. 2006), but pseudo-absences contain an inestimable amount of false absences (Chefaoui and Lobo 2008), thus biasing comparisons. Although presence-only data are effective in many cases at defining species ranges (Elith et al. 2006), they can result in vast over-prediction of occurrence (Lütolf et al. 2006) and generally do not perform as well as models that include non-detections (Brotons et al. 2004, Elith et al. 2006).

Other types of historical data include presence and non-detection data, where each site was visited once and all species detected were recorded (Table 1). Presence and non-detection data are more informative than presence-only data and can give estimates of changes in occupancy (Parsons et al. 2008). However, the inability to discriminate non-detections from true absences means naïve use of presence and non-detection data overestimates colonization events and underestimates extinction events (MacKenzie et al. 2003). To yield presence and estimable absence data, historical surveys at sites must have been repeated within short time periods, either by one observer or multiple independent observers. Assuming that survey sites do not change occupancy status over short time scales, repeated surveys or collecting events provide patterns of detection and non-detection, enabling the estimation of the probability of true absence given imperfect detection (MacKenzie et al. 2006). Lastly, abundance data enhance simple presence or non-detection data by enabling the estimation of changes in relative abundance, true abundance, or density over time, thus providing a more comprehensive view of range and distribution. Documenting contemporary range change solely through the use of historical abundance data, however, has proven difficult owing to the use of outdated or nonstandard methodologies in collecting most historical abundance data (Shaffer et al. 1998).

No matter the data format, a notable problem with historical data is the difficulty in differentiating between true absences and non-detections. In particular, the burden of evidence necessary to define "extinction" has been discussed for a variety of taxa (Newmark 1996, La Marca et al. 2005, Kery et al. 2006). In at least one case (Britten et al. 1994), populations presumed extinct were re-discovered during the publication process because populations were too low during the original survey period for the species to be detected, highlighting the dangers of presuming a non-detection to be equivalent to an absence. Consequently, detectability has a key role in interpreting non-detection data (Kery 2002).

Whereas false absences are a well-documented and consistent problem for interpreting occurrence data, "false presences" or misclassifications of species, are generally ignored. False presences are typically associated with survey data, where species identification is related to individual observer skill and experience (Southgate et al. 2005). However, analyses of range based on physical specimens are not immune from false presences, as misidentifications of specimens in museums (Townson et al. 1999, Graham et al. 2008) and herbaria (Miller et al. 2007) have occurred. Although misidentifications of specimen records can be secondarily validated, correcting for false presences in survey work is more complicated. Meeting this challenge is necessary, however, as even low rates of false presences in occurrence data can bias estimated distributions (Royle and Link 2006).

A broader problem inherent to all historical data arises from the comparability of surveys done at different times with "different underlying properties" (Shoo et al. 2006). Comparing occurrence data from different time periods often suffers from survey-specific differences in methodology, observer skill, weather, effort and other related factors. Thus, comparisons between historical and modern data will often have more inherent bias than comparisons between samples taken within a single time period (Hilden 1981).

Finally, geographical precision is a problem typically unique to historical occurrence data, yet has been largely ignored. Museum specimens are usually georeferenced by referring to specimen tags or collectors' field notes, but vague accounts, dishonest reporting and human error have led to inaccuracy or imprecision in location (Peterson et al. 2004). These biases might exist unrecognized, despite new protocols to incorporate estimates of locational uncertainty consistently into georeferencing processes (e.g., Guo et al. 2008). Locational error can create inaccurate distribution maps (Graham et al. 2008) and can impact estimates of species richness and community composition (Rowe 2005). In resurvey work, locational error can lead to false conclusions on extinction and colonization events, inflating turnover estimates (Miller et al. 2007).

Past attempts to account for problems with historical occurrence data

The use of historical surveys for range change comparisons has grown rapidly. Ten years ago, Shaffer et al. (1998) championed the use of historical data to document declines, citing 15 studies over 38 years that resurveyed species distributions. To illustrate the variety of inferences available from historical data and how they were made, we reviewed recent work published since Shaffer et al. (1998) that explicitly compared historical and contemporary survey data (Table 2). We found 37 studies published over the past decade that resurveyed species distributions. The time period separating historical and contemporary data varied among studies, depending largely on the data source. Generally, the longest durations were studies of plants in isolated patches (Stehlik et al. 2007, Primack et al. 2009). Only one study used historical data to examine colonization (Loo et al. 2007), despite the existence of a large literature on colonization and species invasions (c.f., Mack et al. 2000)). Consequently, many researchers do not appreciate the value of conditioning current presences with probabilistic assessment of past absence.

Many of the biases inherent in the use of historical occurrence data were not acknowledged in past studies. Almost two-thirds of the recent studies resurveyed specific locations where historical data were collected (i.e. sampling sites as fixed effects; Shaffer et al. 1998), whereas the remainder resurveyed in the same region, foregoing a direct site-to-site comparison (i.e. sampling sites as random effects; Shaffer et al. 1998). More than half of the studies (54%) acknowledged that data collection methods differed between the resurvey and the historical survey, and that this might have affected detectability of species; yet, only one study (Moritz et al. 2008) attempted to correct for this problem. Even fewer studies (35%) discussed the risk of false absences in historical or resurvey data, and these primarily dealt with proving extinctions rather than range change. Only three studies statistically quantified the probability of false absences in occurrence data.

In conclusion, although some researchers were aware of problems caused by using historical data, most failed to address them directly. It is likely that the complexity of the problems and the novelty of accessible solutions are mostly to blame for the widespread lack of response to biases in historical data.

Dealing with problems in historical occurrence data: a primer

Some issues with historical data, particularly geographic precision and survey-specific differences, can be addressed simply through careful design of resurvey efforts (Strayer and Fetterman 1999). For example, sites with extreme uncertainty in location can be removed from analysis (McPherson et al. 2004). Additionally, by conducting modern surveys at the same location, time of day and time of year as the historical data, many potential biases of comparison can be reduced. However, even perfect matching of survey characteristics and methods cannot eliminate large differences in detectability between sampling periods, and these differences must be approached in a separate manner.

Many factors – both controlled (e.g., survey method, time, and date) and uncontrolled (e.g., weather, habitat) – can impact the probability of detecting a species, and the degree of impact can differ on temporal, geographic and taxonomic scales (Kery 2002, Bailey et al. 2004, Alldredge et al. 2007). Thus, species will often differ in probabilities of detection, which might be site-, era-, or survey-specific. Expecting differences in detectability between survey eras enables development of sets of hypotheses that can be tested using occurrence data. The "occupancy modeling" approach simultaneously estimates both the probability of detection and the probability of occupancy, conditioning probabilities of occupancy with the risk of false absences (MacKenzie et al. 2002, MacKenzie et al. 2003, MacKenzie et al. 2006). This approach can model covariates of both occupancy and detectability, enabling separate, independent estimates of detection and occupancy for survey eras, or independent probabilities of detection for survey methods (Nichols et al. 2008). A strength of this framework lies in testing and comparing competing models that represent hypotheses of which covariates best explain the observed patterns of detection or occupancy (Burnham and Anderson 2002).

Occupancy models cannot use presence-only data but require repeated surveys at the same locations within a time period to estimate detectability (MacKenzie et al. 2006). If historical presence and non-detection data without repeated surveys are available, detectability functions derived from modern repeated survey data could be applied to historical non-detections, but it is ill-advised to assume that detectability is constant across survey eras.

Although the application of occupancy modeling is expanding rapidly, its use to compare modern and historical data is still rare (Moritz et al. 2008). Given the complex and variable nature of historical occurrence data, a flexible framework for analysis is needed. We highlight two different methods ("unpaired" and "paired" site models, Box 2) for comparing occupancy at sites between historical and modern eras. Each asks slightly different questions of occurrence data, yet both facilitate the estimation of range shifts while accounting for risks of false absence.

Although both models consequently solve many issues in using historical data, neither addresses the problem of false presences. At least one modification to occupancy models enables incorporation of false positives (Royle and Link 2006) by estimating the probability of a false positive at a site where a species is not present. Modeling the probability of false positives reduces inflated estimates of occupancy when false positives are abundant (Royle and Link 2006). Consequently, models incorporating the risk of false positives should be strongly considered when analyzing occurrence data. However, this is a developing field and methods that further integrate false positive risks into the occupancy modeling framework are needed.

Measures of range change

Estimating the probability of occupancy for a species in both historical and present eras accounts for many of the biases in historical data, yet a method is also needed to measure range change. Defining the range of a species is a complex and often controversial task (Brown et al. 1996); consequently, we provide multiple methods for comparing ranges across time. The first method requires a modeled probability of detection function, whereas the second method could be applied to any occupancy distribution.

The first method examines naïve estimates of change in occupancy and tests for statistical support by calculating the Probability of False Absence (P_{fa}). This measure comes from Moritz et al. (2008), and is reformulated as Equation 1:

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

where p_{ij} is the probability of detection at the *i*th 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 can be calculated across *m* sites with non-detections to estimate the chance the species was present at all of those sites and escaped detection. The P_{fa} test uses only the modeled probabilities of detection to test the likelihood of absence across a set of unoccupied sites. Consequently, it gives a confidence estimate of whether a naïve range shift is significant.

Of many possible uses, P_{fa} tests have been used to test for changes in the limits of distributions (Box 3) (Moritz et al. 2008). However, inferences focusing solely on the limits or extremes of a distribution could be biased by vagrant or single "out-of-range" individuals that temporarily exist outside the boundary of the fundamental niche (Grinnell 1922). These individuals might signify "sink" populations that cause an apparent expansion of range boundaries (Pulliam 1988), or result in observed high rates of turnover and local extinction at range boundaries (Doherty et al. 2003). Although individuals or populations at the limits of a distribution might most responsive to environmental change, occupancy changes across the whole of a species distribution might be more indicative of a population-level response to environmental change (Archaux 2004). In simulations, analyses of range change based on entire distributions have been shown to be more sensitive to detecting expansions or retractions than have analyses focused on range limits (Shoo et al. 2006).

In attempting to infer change from the entire distribution, several authors (Wilson et al. 2005, Lenoir et al. 2008) have used a "maximum probability" approach, where the maximum probability of occupancy in a species distribution along a gradient (elevation) was chosen as the species "optimum" (Box 3). Changes over time can be calculated as shifts of the species optimum (Lenoir et al. 2008). Although this approach provides inference on the distribution as a whole, it is difficult to interpret when there is no single maximum value (e.g. when occupancy is maximized over many continuous values or the distribution is multi-modal). The development of further measures for estimating range shift from probabilistic occupancy functions should be a priority for future research in applying these analytical methods.

Conclusions: an eye to the past and an eye to the future

Many of the problems with using historical data can now be explicitly accounted for through occupancy modeling (MacKenzie et al. 2006) and other quantitative techniques (Moritz et al. 2008). To avoid bias, however, these techniques require, at a minimum, occurrence data with some repeated visits within survey periods, and data from enough sites to achieve sufficient statistical power (c.f., Bailey et al. 2007). Consequently, occupancy modeling is not a "one-size-fits-all" solution and additional approaches will need to be developed to deal with all types of occurrence data (Table 1). The recent development of "multi-state" occupancy models (MacKenzie et al. 2009) may provide a useful framework for comparing historical and resurvey abundance data.

The tools presented here provide important implications for those who both store and use historical data, as well as those who collect contemporary data. Foremost, observational and occurrence data should be given greater value by NHMs, field biologists and other holders of original historical records. In particular, field notes often hold key occurrence metadata, including information on non-detections, location and effort, that individual records do not contain. When possible, occurrence data, including field notes, should be made publicly available and important metadata, such as geographic location and specificity, should be refined and uncertainty quantified. NHMs have led the way in making specimen-based occurrence data available publicly (Graham et al. 2004), but have been slow to do the same with historical observation records.

To estimate probabilities of detection, museums or database managers might have to modify how occurrence records are related to each other in a structured database (Porter 2000). Most specimen-based occurrence databases are currently structured around localities, with specimens attached to localities, and items such as collection date and collector are unrelated metadata (Canhos et al. 2004). To estimate detectability, occurrence records need to be assembled into survey periods, with resurveys at localities. Thus, date of collection and collector become crucial organizational levels of occurrence data rather than unrelated metadata. Incorporating this extra structural level into databases might be difficult to populate with data correctly, particularly as most occurrence databases are organized around known objects (e.g., specimens or observations) rather than non-detections. Designating occurrence data as part of a specific "survey" or "collection event" requires detailed historical records and the effort to obtain them (Graham et al. 2004). Conversion from presence-only occurrence data to presence and estimable absence data (Jones et al. 2006) would be a burden on NHMs, which have other important missions. Yet, this endeavor would expand the value of museum specimens and records for measuring the influence of environmental change.

To increase the future value of contemporary occurrence or specimen data, researchers could organize their sampling efforts to include repeated surveys to estimate detection probabilities. Repeatedly surveying locations during a single collecting trip conflicts with conventional museum collecting methods, which sample as many habitats and locations as possible to maximize diversity of collections. Yet, changing methods to include repeat surveys is necessary if researchers are to infer absence successfully and thus accurately estimate occupancy. If resampling specific transects is not possible, sampling similar habitats within the same locality can facilitate estimation of detectability at a local level.

Historical data represent an underused but valuable source of data that can provide novel insights into how the natural world has changed over human life spans. The rapid pace of human-mediated alteration of the global environment demands that ecologists turn to innovative methods for identifying impacts (Sparks 2007). By enlarging established baseline data sets to include historical data, researchers can expand both the geographic and the temporal scale of inference on change. To do otherwise would forfeit countless opportunities to gain reliable knowledge about biological processes on time scales that have been largely unstudied.

Glossary

Absence: a species not occurring at a location (site), difficult in practice to differentiate from a non-detection.

Colonization: an event where a location transitions from being unoccupied to being occupied by a species over time.

Covariate: an explanatory variable that is potentially predictive of the studied outcome. Covariates might be directly related to occupancy (e.g. elevation or habitat) or important nuisance terms affecting detectability (e.g. era or season) that need to be controlled.

Detectability: the probability that a species will be found (detected) during a survey given its presence.

Extinction: an event where a location transitions from being occupied to being unoccupied by a species over time.

False absence: a non-detection that is treated mistakenly and with certainty as a true absence.

Georeference: a specific reference in a geographical coordinate system that assigns an event (e.g. a detection or occurrence) to a location.

Gradient: a measurable physical quantity or dimension (e.g. elevation, temperature or longitude) that changes gradually in magnitude.

Non-detection: when a species was not detected during a survey by the observer. Non-detections result from the species either being absent or being present and undetected.

Occupancy: the probability of species being present at a set of locations.

Occupancy modeling: an analytical framework that estimates the probability of occupancy while taking into account imperfect detection during surveys. It is summarized in Mackenzie et al. (2006).

Presence: a species occurring at a location, as affirmed by a positive detection.

Resurvey: a survey that returns to an area that has been previously surveyed. Used to estimate detectability when the time interval between surveys is very short, and to make comparisons between two or more time periods (eras) when the interval between surveys is long.

Season: in reference to occupancy modeling, a season refers to any duration of time within which occupancy does not change, but between seasons occupancy can change (MacKenzie et al. 2006). Single-season occupancy models only estimate the probability of occupancy for a single season. Multiple-season occupancy models estimate an initial probability of occupancy for the first season and then estimate concurrent probabilities of extinction and colonization for subsequent seasons.

Box 1. Defining “historical occurrence data”

We define historical occurrence data as any set of information that provides evidence on the presence or absence of a species. The term “historical” is relative yet implies that the individual who collected the occurrence records in the past might differ from the person using the records in the present. We also distinguish historical occurrence data from long-term monitoring data, which is often highly standardized, measured and specific in purpose. By contrast, historical occurrence data can be anecdotal, observational and general in nature. To be used in understanding species ranges, historical occurrence data must contain information on at least location and time. Without an assigned geographic locality and temporal reference, occurrence records cannot be compared to contemporary data.

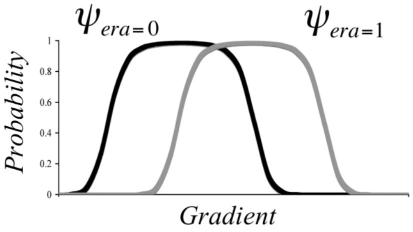
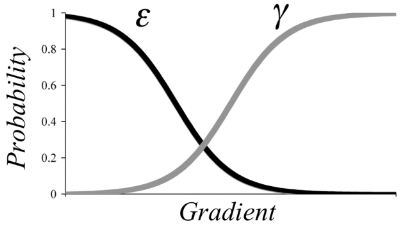
Historical occurrence records originate from a variety of sources. Faunal surveys, such as for breeding atlases (e.g., Hill et al. 2002), are the most obvious source of data, as they were originally collected with the purpose of estimating species distributions. Historical species accounts and species lists can also be found in the field notes and journals of observers who collected the data without an intentional immediate use. In some cases, photographs of a specific location (e.g., Martin et al. 2004, Miller-Rushing et al. 2006, Danby and Hik 2007) can be sources of occurrence data for visually unique species, tree species, habitat elements, or other aspects of vegetation. Finally, specimen collections from natural history museums are highly valuable sources of information on species occurrence (Suarez and Tsutsui 2004). Metadata from specimen records are increasingly available over the Internet from global museum databases (e.g. VertNet, http://vertnet.org/) which enable rapid access to large amounts of occurrence data from around the world (Graham et al. 2004).

Box 2. Parameterizations of occupancy models for inferring range shifts

The unpaired-site model provides a flexible framework with which to work with occurrence data (Table I). With the unpaired-site model, data from all sites are entered into a single-season occupancy design (MacKenzie et al. 2006) and “era” (e.g. historical surveys or modern resurveys) is a covariate explored in both models of detectability and occupancy. This configuration does not require matched pairs of sites, but does require occupancy to be related to a defining covariate affecting range (e.g. elevation, precipitation, latitude, or longitude). Many different mathematical forms can be used to model the relationship between occupancy and a covariate. Change in the relationship between this defining covariate and occupancy is used to create occupancy profiles and is examined as a proxy for colonization or extinction at sites (Moritz et al. 2008). Consequently, the unpaired-site model can be used when historical locations are not described well enough to enable a matched pair analysis, and when the relationship between a species and an environmental gradient is the desired indicator of change over time. It is also useful when the number of paired sites sampled and the number of sites changing occupancy state are small.

The paired-site model can be used to explore occupancy when sufficient numbers of matched pairs of sites are available (Table I). In this specification, a “multi-season” occupancy design (MacKenzie et al. 2006) is used to compare how the probability of colonization and extinction of sites has changed occupancy between eras. The paired-site model typically estimates the probability of historical occupancy at a site and then models the probability of extinction and colonization between eras (MacKenzie et al. 2003). Site-specific covariates (e.g. changes in climate or land use) can be used to explore specific hypotheses related to colonization and extinction estimates. The paired-site model might enable a mechanistic analysis of the factors that affect site-specific occupancy by incorporating covariates potentially associated with range change.

Box 2. Table I. Model parameterizations for occupancy comparisons along a dominant gradient over two time periods[a].

Model	Modeled parameters	Example equations	Range change inference
Unpaired site	Occupancy (ψ) Detectability (p)	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot gradient + \beta_3 \cdot gradient^2$ $\text{logit}(p) = \beta_4 + \beta_5 \cdot era$	
Paired site[b]	Initial Occupancy (ψ_0) Extinction (ε) Colonization (γ) Detectability (p)	$\text{logit}(\psi_0) = \beta_0 + \beta_1 \cdot gradient + \beta_2 \cdot gradient^2$ $\text{logit}(\varepsilon) = \beta_3 + \beta_4 \cdot gradient$ $\text{logit}(\gamma) = \beta_5 + \beta_6 \cdot gradient$ $\text{logit}(p) = \beta_7 + \beta_8 \cdot era$	

[a] Time, or era, is a covariate with which occupancy and/or detectability might vary.

[b] Extinction (ε) and colonization (γ) probabilities enable calculation of occupancy in future time periods from an initial probability of occupancy (ψ_0) and a probability of detection (p), which might or might not be era specific.

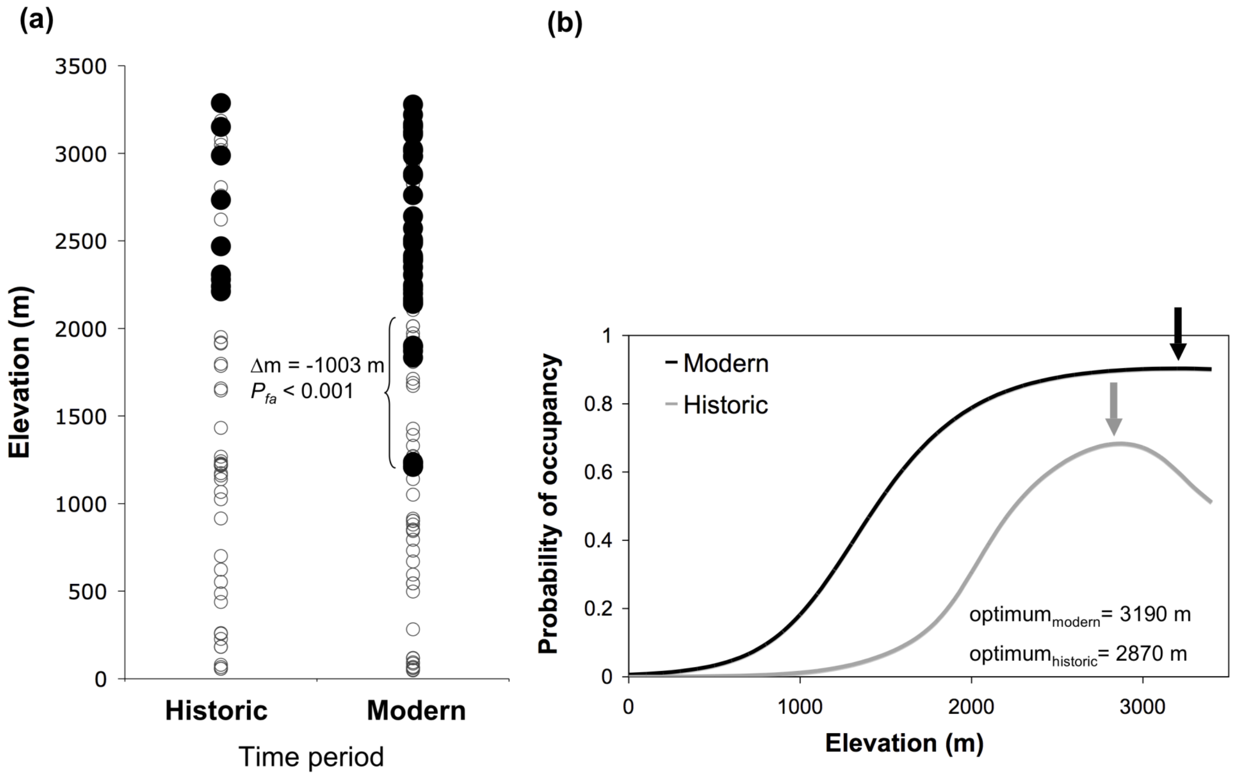
Box 3. Measuring range changes in practice

We use the montane shrew, *Sorex monticolus*, to illustrate two ways of measuring range change via occupancy modeling. Our data come from Moritz et al. (2008) in which small mammal communities were resurveyed along an elevational transect through Yosemite National Park, USA. Historical surveys of small mammals were conducted by trapping at sites on consecutive nights, thus building a record of repeated surveys. Due to the inability of the resurvey team to locate all historical sites with high confidence and to the addition of new survey sites, the unpaired-site model was used for analyses.

Moritz et al. (2008) defined and categorized range shifts through the use of P_{fa} tests (Figure Ia). Detectability was estimated using the best of 32 competing models that explored changes in detectability over trap night and survey era, and included trap effort. Historically, *S. monticolus* was not found below 2212 m. During the resurvey, it was found at 18 lower sites, down to 1209 m. The probability that *S. monticolus* was present within that elevational range at one or more of the historical survey sites (n=17) and went undetected in the contemporary resurvey was $P_{fa} < 0.001$. Consequently, it was concluded that the lower elevational range limit of the species had shifted downward by 1003 m.

Another way to examine range shifts is through species optimums, by determining the covariate value where the probability of occupancy is highest (Wilson et al. 2005, Lenoir et al. 2008). Moritz et al. (2008) built a candidate set of 112 occupancy models per species using the best 14 detection models combined with 8 competing occupancy models that incorporated era, elevation represented as linear or quadratic functions, and interactions. Model-averaged occupancy curves (Burnham and Anderson 2002) were created for *S. monticolus*, illustrating how the probability of occupancy changed over the elevational gradient and how this relationship changed over time (Figure Ib). Historically, the optimum elevation was at 2870 m, whereas the modern optimum increased to 3190 m, an increase in optimum elevation of 320 m. *S. monticolus* occupancy also increased throughout its range.

At first glance, these two measures seem to provide contradictory conclusions from the same data. However, they describe different aspects of the complex process of range change. Looking at either the range margins (P_{fa}) or the optimum partially describes range change, yet neither measure describes change to the entire range. Lack of a standard technique to compare full range distributions hinders our ability to understand how species have responded to large-scale environmental change.



Box 3. Figure I. Methods of quantifying range change using modeled probabilities of detection and occupancy for the species *Sorex monticolus* (Moritz et al. 2008). Raw presence (solid circle) and non-detection (open circle) data (a) can be used to calculate the probability of false absence (P_{fa}) for a set of sites along an elevational gradient. The modeled probability of occupancy curve (b) can be used to find the "optimum" elevation (denoted by arrows) for each time period. Figure adapted from the online Supplementary Material in Moritz et al. (2008).

Table 1. Different types of historical occurrence data listed from least informative to most informative.

Extent of occurrence data	Data depiction[a]			Non-detection data	Temporal replication	Inference available	Biases to range estimation
		$Survey_1$	$Survey_2$				
Presence-only	$Site_i$	●	—	No	No	Extinction only	Pseudo-absence data lead to overprediction of historical range and of extinction, and no inference on colonization
	$Site_j$	●	—				
	$Site_k$	—	—				
Presence and non-detection		●	—	Yes	No	Extinction and colonization	False absences give underprediction of historical range and extinction and overprediction of colonization
		●	—				
		○	—				
Presence and estimable absence		●	●	Yes	Yes	Extinction and colonization	Probability of occupancy reduces false absence bias
		●	○				
		○	●				
Abundance		⓮	⓴	Yes	Yes	Extinction, colonization and change in population size	False absence bias reduced, but abundance comparisons bring new set of biases
		❶	○				
		○	❸				

[a] Open circles represent sites where a species went undetected during historical surveys, whereas closed circles represent sites with detections. Numbers in the circles represent abundances. Data presented for illustrative purposes only.

Table 2. Recent studies that have explicitly resurveyed historical data to make different types of inference on range change.

Study system	Location	Historical data source	Time span of comparison[a]	Addressed biases?			Refs
				Attempted resurvey of specific localities[b]	Addressed differences in methodology or similar factors[c]	Addressed false absences[c]	
Exinction only							
Plants	Oceania	Literature	99 - 114	Yes	No	No	Duncan and Young 2000
	Europe	Specimens	5 - 127	Yes	No	Verbally	Lienert et al. 2002
	Europe	Specimens	88 - 164	Yes	No	Verbally	Stehlik et al. 2007
	Europe	Literature	80 - 100	Yes	Verbally	Statistically	Kery et al. 2006
	Africa	Specimens	12 - 131	No	No	Verbally	Hanski et al. 2007
Mammals	North America	Specimens, literature, field notes	60 - 129	Yes	No	Verbally	Larrucea and Brussard 2008
Colonization only							
Snails	Australia	Specimens, literature, field notes	110	No	Verbally	No	Loo et al. 2007
Extinction & colonization							
Amphibians	North America	Specimens, literature	27 - 106	No	No	No	Bradford et al. 2005
	North America	Original survey data, pers. comm.	21 - 29	Yes	Verbally	Verbally	Gibbs et al. 2005
	North America	Specimens, literature	22 - 82	No	Verbally	Verbally	Hossack et al. 2005
Birds	Africa	Literature	30 - 47	Yes	Verbally	No	Azeria et al. 2006
	Europe	Literature	28 - 38	Yes	Verbally	Verbally	Foufopoulos and Mayer 2007
Range change[d]							
Algae	Europe	Literature	32 - 50	Yes	Verbally	No	Lima et al. 2007
Trees	Europe	Literature	45 - 55	Yes	No	No	Kullman 2002
	North America	Original survey data	62 - 71	Yes	No	No	Franklin et al. 2004
Plants	Europe	Atlas	115	Yes	Verbally	No	Lavergne et al. 2005
	Europe	Original survey data	1 - 100	No	No	No	Lenoir et al. 2008
	North America	Original survey data, pers. comm.	28 - 29	Yes	Verbally	No	Kelly and Goulden 2008
	North America	Field notes, literature	40 - 183	Yes	Verbally	Verbally	Primack et al. 2009
Coral	Oceania	Field notes, literature	82 - 85	Yes	Verbally	No	Cornish and DiDonato 2004
Bivalves	North America	Field notes, literature	31 - 42	Yes	Verbally	Verbally	Strayer and Fetterman 1999
Lepidoptera	Europe	Atlas	5 - 35	No	No	No	Franco et al. 2006
	Europe	Pers. comm., literature	31 - 37	Yes	No	No	Wilson et al. 2005
	Europe	Atlas	15 - 51	No	No	No	Konvicka et al. 2003
Odonata	Europe	Atlas	15 - 35	No	Verbally	No	Hickling et al. 2005

Amphibians	North America	Specimens, literature, field notes	13 - 119	Yes	Verbally	Statistically	Davidson et al. 2001
	North America	Field notes, specimens	30	Yes	Verbally	No	Lips et al. 2004
	South America	Literature	18 - 34	Yes	Verbally	No	Ron et al. 2003
	North America	Pers. comm., literature	22 - 33	Yes	No	No	Skelly et al. 2003
Herpetofauna	North America	Original survey data, literature	61 - 66	No	No	No	Brodman et al. 2002
Birds	North America	Field notes, specimens, pers. comm.	51 - 93	No	Verbally	No	Martin et al. 2004
	North America	Field notes, literature	38-83	No	No	No	Winker et al. 2002
	Europe	Atlas	7 - 15	No	No	No	Brommer 2004
	Europe	Atlas	16 - 23	No	No	No	Thomas and Lennon 1999
Mammals	North America	Field notes, specimens	83 - 94	Yes	Statistically	Statistically	Moritz et al. 2008
	North America	Field notes, specimens	1 - 125	No	Verbally	Verbally	Myers et al. 2009
	North America	Field notes, specimens	51	Yes	Verbally	No	Rowe 2007

[a] Time span calculated as minimum to maximum number of years between historical and contemporary data. For instance, data collected between 1920-1930 and 2000-2005 would equal 70-85 years of time span.

[b] Distinction was made between a resurvey at the same location as historical data and resurveying in the same general vicinity but not a direct comparison of occupancy at the site level (Shaffer et al. 1998).

[c] A verbal address acknowledges the inherent bias and might or might not try to explain how the problem was mitigated; a statistical address attempts to control for the bias through any variety of statistical methods.

[d] Range change was identified as a resurvey study where the goal was to look at the change in geographical range of a species over time. This was considered distinct from an extinction and colonization study where the goal was to look at occupancy dynamics or turnover within a population.

Chapter 2.

Birds track their Grinnellian niche through a century of climate change

This article has been published previously and is reproduced here with permission from the publisher, the National Academy of Sciences of the United States of America:

Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences, 106(suppl. 2): 19637-19643.

Abstract

In the face of environmental change, species can evolve new physiological tolerances to cope with altered climatic conditions, or move spatially to maintain existing physiological associations with particular climates that define each species' climatic niche. When environmental change occurs over short temporal and large spatial scales, vagile species are expected to move geographically by tracking their climatic niches through time. Here we test for evidence of niche tracking in bird species of the Sierra Nevada mountains of California, focusing on 53 species resurveyed nearly a century apart at 82 sites on four elevational transects. Changes in climate and bird distributions resulted in focal species shifting their average climatological range over time. By comparing the directions of these shifts relative to the centroids of species' range-wide climatic niches, we found that 48 species (90.6%) tracked their climatic niche. Analysis of niche sensitivity on an independent set of occurrence data significantly predicted the temperature and precipitation gradients tracked by species. Furthermore, in 50 species (94.3%), site-specific occupancy models showed that the position of each site relative to the climatic niche centroid explained colonization and extinction probabilities better than a null model with constant probabilities. Combined, our results indicate that the factors limiting a bird species' range in the Sierra Nevada in the early 20th century also tended to drive changes in distribution over time, suggesting that climatic models derived from niche theory might be used successfully to forecast where and how to conserve species in the face of climate change.

Introduction

Nearly a century ago, Joseph Grinnell presented the concept of the ecological niche as the primary determinant of a species' range (Grinnell 1917b). Grinnell defined the niche as a set of environmental conditions that restricts each species, through "physiological and psychological respects" (Grinnell 1917b), to a geographical range where it can prosper. In particular, Grinnell discussed the important role played by temperature in ultimately defining range boundaries, but noted that within the limits of physiological tolerance, numerous factors – including interspecific competition – can determine realized range boundaries (Grinnell 1917a). Since Grinnell, empirical explorations of species' range determinants have successfully related environmental limits to range boundaries through physiological knowledge (Root 1988). At the same time, field and laboratory experiments have demonstrated that species interactions may also limit ranges (Davis et al. 1998b, Suttle et al. 2007), and that climatic associations can rapidly change when species are introduced to new environments (Broennimann et al. 2007). Nevertheless, the concept that environmental limiting factors define the niche where a species can have a positive growth rate still remains the dominant explanation for range boundaries (Holt et al. 2005), suggesting that the spatial extent of the range for most species is approximately equal to the geographical expression of a species' niche (Brown et al. 1996).

Temporal sampling of changing environments makes it possible to measure the dynamic relationship between the environment, a species' climatic requirements, and its realized range. If ranges are shaped by physiological limitations that remain fixed over the time-scale of comparison, then species ranges should also move across the landscape as averages and extremes of temperature, precipitation and relative humidity change over short time spans (Graham et al. 1996, Jackson and Overpeck 2000, Peterson 2003). This process, by which species follow limiting environmental boundaries through geographical space to remain in a favorable climatic space, is called niche tracking (Graham et al. 1996, Martinez-Meyer et al. 2004, Monahan and Hijmans 2008). Niche tracking can occur when a local population in unfavorable climate conditions becomes extinct, or when individuals colonize sites in newly favorable climates. Studies of both recent and paleontological climate change have examined niche tracking through range changes (Root et al. 2003, Parmesan et al. 2005). If species track niches limited by temperature, then they should move upward in elevation or poleward in latitude as the climate warms. A global meta-analysis of 434 species that have shifted ranges indicated that 81% of species showed this expected pattern in response to recent climate change (Parmesan and Yohe 2003). However, 19% moved in directions opposite that predicted by temperature, and many others did not change range. Studies that have explored life history factors as potential correlates of movement patterns have found no simple explanation (Moritz et al. 2008), and there is little empirical evidence for why species show heterogeneous responses (Parmesan et al. 2005).

A more direct approach to examining the role of the niche in driving species response to climate change is necessary if these seemingly contradictory patterns are to be understood. Analyses of shifts in elevational or latitudinal range are used as proxies for shifting temperature gradients (Parmesan 2006), yet niches can be defined by any set of abiotic factors that may or may not covary with elevation or latitude (Hutchinson 1957, Chase and Leibold 2003). If the role of the niche in dynamically determining ranges is to be understood, multiple environmental facets of the niche need to be explored. Modern resurveys of areas with historical occurrence data provide unique opportunities to empirically test the role of niche tracking in driving species-specific responses to climate change (Wiens and Graham 2005).

Here we use a unique dataset of changes in avian site occupancy over the past century to test the degree to which 53 bird species distributed across an elevational gradient track a two-variable environmental niche through space and time. We expect species to have responded to climate change by modifying their ranges to remain within their pre-existing climatic niche. Our data come from historical (1911-1929) surveys and contemporary (2003-2008) resurveys of 82 sites along four elevational transects throughout the Sierra Nevada of California, USA (Fig. 1). These sites have seen an average change in breeding season climate towards warmer (+0.80 ± 0.07 °C, mean ± s.e.) and wetter (+5.90 ± 0.57 mm) conditions, revealing an overall increase in ecosystem net primary productivity (NPP). We examined changes in climatological range and site occupancy between the two survey periods and how these changes related to the climatic niches of species. We tested: (*i*) whether species have, on average, tracked their climatic niche over time (i.e., climatic range centroids means moving toward the niche centroid, not away from it); (*ii*) if environmental gradients tracked by a species can be predicted *a priori* based on climatological factors limiting historical distributions; and (*iii*) if colonization and extinction probabilities at sites are modeled well by a site's climatological position relative to the niche centroid.

Defining the climatic niche and quantifying niche tracking

Hutchinson (Hutchinson 1957) formalized the idea that the niche can be partitioned into the fundamental and realized portions. However, there is disagreement on whether the fundamental niche can be inferred from species occurrences (Peterson et al. 1999, Soberón and Peterson 2005), or can only be measured from mechanistic analyses of physiological tolerances (Davis et al. 1998b, Kearney and Porter 2009). Our goal here is not to define the complete *n*-dimensional environmental niche for each species, but to determine an approximate set of climatic conditions in which species can occur, also known as the Grinnellian niche (Soberon 2007). Analyses of climatic conditions throughout entire ranges of species theoretically provide suitable approximations of these conditions (Araújo and Guisan 2006)}. Furthermore, niche centroids provide measures of the distributional center of favorable climatic conditions (Broennimann et al. 2007), avoiding the difficulties inherent in measuring and interpreting range boundaries in climate space (Guisan and Thuiller 2005, Kearney 2006). For instance, both source-sink dynamics (Pulliam 2000) and the graded response of fitness to environmental conditions (Holt and Gaines 1992) might blur the appearance of a hard niche boundary. Consequently, we used the average historical temperature and precipitation observed across an entire species' range, as delimited by occurrences of historical (1860-1940) museum specimens, as the centroid of its climatic niche.

Range change, and thus the ability of species to track their climatic niche, occurs at two primary spatial scales. At the scale of the site where individuals live, niche tracking during environmental change can lead to three outcomes (Jackson and Overpeck 2000) (Fig. 2a). First, the site may remain within the climatic niche of the species despite climate change, allowing individuals to continue occupying it. Second, the local environment may shift outside of the climatic niche, leading to extinction at the site through reduced survival or reproductive success, or emigration. Third, the local environment may shift inside the climatic niche, allowing colonization if dispersal occurs. Depending on the time scale, the magnitude of environmental change, the size of the niche, the "hardness" of niche boundaries, and other natural history characteristics of the organism, any or all of these outcomes may be expected results of climate change at the site-level. Combinations of outcomes at sites are realized geographically as contractions, expansions, or stasis at the scale of the range (Jackson and Overpeck 2000). Thus, changes in site occupancy driven by changing environmental conditions are manifested as range shifts (Anderson et al. 2009).

At both the site and range scales, empirical data can be used to explore whether outcomes are related to climatic changes relative to the niche. Given that the climate has generally become warmer and wetter in our study region over the last century (Bonfils et al. 2008a, Parra and Monahan 2008), although with varying geographical context (Fig. 1b), a species showing geographic range stasis would exhibit movement of their climatic range toward a warmer and wetter environment. If species do track their climatic niche, then this outcome would only be expected if warmer and wetter conditions were favorable; that is, the centroid of their climatic niche is warmer and wetter than where the species occurred before environmental change. In contrast, if climatic conditions shift away from the niche centroid, vagile species might adjust their occupancy by colonizing newly favorable sites or abandoning unfavorable sites (Araújo et al. 2006). This would result in an occupied range that tracks the climatic niche, despite the inertia of environmental change.

We first tested at the regional scale whether species tracked their climatic niche over time or moved independently. For each species we examined whether a temperature or precipitation shift in observed range mean ($\mathbf{R}_T$ and $\mathbf{R}_P$; Fig. 2b) matched in sign with the environmental direction from the niche centroid to the observed historical range mean ($\mathbf{H}_T$ and $\mathbf{H}_P$; Fig. 2b, Table S1). For example, if the climatic niche centroid is cooler and wetter (e.g., Fig. 2d) than the mean environment of the observed historical range, then an observed modern range that is also cooler and wetter than where the species was found historically would provide evidence for niche tracking on both axes.

We then examined site-specific occupancy dynamics as a predictive driver for niche tracking throughout a range. The occupancy modeling framework (MacKenzie et al. 2006) allowed us to estimate colonization and extinction probabilities for sites, while taking into account the risk of false absences. Three models were used to test how turnover of occupancy related to the climatic position of sites relative to the climatic niche of a species (Fig. 3). In the null model (Fig. 3a), all sites have the same probability of changing occupancy status, implying that the climatic niche has no association with colonization-extinction dynamics. Alternatively, the static model assumes the magnitude of environmental shift from climate change is small relative to the distance from occupied sites to a species' climatic niche. In this case, the climatic niche does impact colonization-extinction dynamics, but without a significant change in climate, tracking of the niche across climate space is not observed. Consequently, sites in the core of the climatic niche will remain occupied, while peripheral sites on the margin of climatic suitability will exhibit non-directional turnover that is typical of a range at equilibrium (Holt et al. 2005) (Fig. 3b). As the magnitude of environmental shift increases, however, the fate of sites depends on the direction of climate change, and the position of that site in climate space relative to the species' climatic niche. Thus, the dynamic model assumes that sites in the core of the climatic niche mostly remain occupied, while peripheral site dynamics depend on whether climate is pushing the site toward or away from the core (Anderson et al. 2009) (Fig. 3c). In geographic space, this directional turnover may result in a range appearing to be in non-equilibrium (Holt et al. 2005). We structured our dynamic model with five different parameterizations (see Methods), each a unique hypothesis of how colonization and extinction might be related to niche-climate dynamics.

Both the static model and the dynamic model represent niche tracking scenarios, but the difference between them lies in the relative role that climate change plays. If the magnitude of climatic shift is great relative to the proximity of sites to the niche centroid, we expect dynamic models to best describe turnover patterns. However, if sites have only shifted a small amount relative to their distance to the niche centroid, then a static model is likely to fit observed patterns better.

Methods

Observational data and species ranges

Historic and modern species observations originated from the Grinnell Resurvey Project, a large-scale multi-taxa resurvey of the vertebrate fauna of the Sierra Nevada (Moritz et al. 2008, Parra and Monahan 2008). Historical observations were made outside of the winter (earliest was March 26 and latest was October 15, with 82% between May 1 – July 31) between 1911 and 1929 at 82 sites along 4 cross-sectional elevational transects (Fig. 1) as part of regular surveys or "pencil censuses" of birds by Joseph Grinnell and colleagues at the Museum of Vertebrate Zoology, University of California, Berkeley. Historical surveys were repeated at 76% of sites, with a maximum of 17 repeat surveys (median = 3). Modern observations entailed resurveys of historical sites using point counts along transects, conducted by five different observers between 2003 and 2008. Variable-distance point counts (Ralph et al. 1995) lasted 7 minutes, and stations were placed a minimum of 250 m apart along routes that followed, as closely as possible, to historic survey paths. Sites were repeatedly surveyed a maximum of 5 times (median = 3) between May 4 and August 25.

Of the 240 total bird species detected during historical and modern surveys, we selected 53 focal species that matched desired criteria. First, we selected species that were restricted primarily to the western United States. Two western-restricted subspecies, formerly considered full species, "Audubon's" Yellow-rumped Wabler (see Table S1 for taxonomy) and the "Red-shafted" Northern Flicker, were also included. Second, species had to occur during both sampling eras at nine or more survey sites, with four exceptions that were added *a priori* for their strong association to the western U.S. and the Sierra Nevada: American Dipper (11 historic sites, 6 modern sites), Anna's Hummingbird (5 sites, 37 sites), California Thrasher (7 sites, 6 sites), and Pacific-Slope Flycatcher (7 sites, 10 sites). Our final group of 53 species were distributed across the elevational range (see Table S1 for average elevations of each species).

Specimen data and the climatic niche

Historical specimen data (1860-1940) used to estimate the climatic niche were assembled from museum collections accessed through ORNIS (http://olla.berkeley.edu/ornisnet/). ORNIS is a data portal that facilitates easy access to over 35 million unique bird records (specimen and observational) housed by 45 different providers. We downloaded all available specimen records for each species. Specimens without georeferences, or with low coordinate precision (<3 decimal places, in decimal degrees), were excluded, as were records post-1940 and specimens collected outside of the breeding season (breeding in California generally occurs between March – August for resident species, and May – July for migrants). Most specimens from most museums do not yet have estimates of georeference uncertainty (Wieczorek et al. 2004), so uncertainty was not used as a criterion for inclusion. Obvious outliers, including vagrants or incorrect georeferences, were also excluded. With the exceptions described previously, all subspecies of each species were used, providing thorough coverage of the entire known geographic range for each species. Geographic coordinates were sorted within species, and duplicate coordinates were eliminated to reduce sampling bias. The average number of unique specimen localities for species was 148 (SD = 63). We used these historical species locations to calculate the centroid of the climatic niche for each species.

Climate data

Monthly mean minimum temperature, mean maximum temperature, and total precipitation were obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM). PRISM is a knowledge-based system that generates monthly by yearly climate surfaces using mathematical interpolation and expert knowledge (Daly et al. 1994, Daly et al. 2002). PRISM data are made freely available at 2.5 arc minute spatial resolution (approximately 4 x 4 km), a scale reasonable for both the specimen and observational data. We used the monthly variables to compute mean estimates of temperature and precipitation during the breeding season (May through July) sampled in both eras (1910-1930 and 1986-2006). We also used estimates of historical annual mean temperature (T) and annual precipitation (P) to determine which of the two original climate variables limited NPP under the Miami model (Leith 1975), where

$$\text{NPP} = \min\left(\frac{3000}{1+e^{1.315-0.1197\cdot T}}, 3000\left(1-e^{-0.000664\cdot P}\right)\right).$$

Historical and modern climate values were extracted for locations of specimen and observational data for use in analyses. While the average breeding season precipitation in the Sierra Nevada is relatively low (max = 83 mm), this variable was highly correlated with average annual precipitation for our sites (r = 0.96 for historical; r = 0.94 for modern). Breeding season temperature was also highly correlated with annual mean temperature (r = 0.99 for historical; r = 0.99 for modern). Breeding season values were used for site-specific climate values, as they provided direct *a priori* links to changes in avian breeding season occurrence.

A priori hypotheses of niche tracking

We used a maximum entropy technique implemented in MaxEnt (Elith et al. 2006, Phillips et al. 2006) to determine *a priori* whether each species' historical range-wide distribution was shaped more by temperature or precipitation. MaxEnt models were developed using standard default settings in version 3.2.1 of the program (automatic selection of response functions; maximum number of background points, 10,000; background, conterminous United States). Climate variables were historical breeding season estimates of mean temperature and precipitation. Models were developed using all spatially unique historical specimen localities for each species. We used the percentage contribution of each variable to the model to develop testable hypotheses of species' niche sensitivity to breeding season temperature versus precipitation. Absolute scores of contribution to variables were not directly comparable within species, so scores were standardized relative to the median contribution of each variable across all species. A species with, for example, a precipitation contribution greater than the median precipitation contribution across all species, would have precipitation selected as an *a priori* predictor of niche sensitivity. All species had either a temperature or a precipitation score greater than the median, and four species had both.

Occupancy modeling

Multi-season occupancy models (MacKenzie et al. 2006) were built to examine site-specific occupancy dynamics as a predictive driver for niche tracking throughout a range. Multi-season occupancy models simultaneously estimate a probability of detection (p), an initial probability of occupancy (ψ_0), a probability of colonization (γ), and a probability of extinction (ε) based on histories of presence and non-detection at sites over time. The strength of these models lies in being able to estimate occupancy parameters while taking into account the probability that a species was present and went undetected at each site which is critical when dealing with historical occurrence data (Moritz et al. 2008).

We fit covariates to occupancy parameters in two stages, following Moritz et al. (2008). First, we ran four detectability models for each species (allowing detectability to vary by survey era or Julian day) with constant (no covariates) models for ψ_0, γ, and ε. Models were compared using AIC (Burnham and Anderson 2002). The best detectability model (highest AIC weight, w_i) for each species was used to parameterize p for all subsequent colonization and extinction models for that species.

Second, eight occupancy models were compared using different combinations of covariates for γ and ε (MacKenzie et al. 2006). The null model (Table 2; Fig. 3a) had no covariates (i.e., constant probability of γ and ε). The static model (Table 2; Fig. 3b) used the temperature and precipitation vectors $\mathbf{h}_\mathrm{T}$ and $\mathbf{h}_\mathrm{P}$ (Fig. 2c), which measure the distance from each site's historic climatic location to each species' niche centroid, as covariates for γ and ε. The dynamic models (Table 2; Fig. 3c) were divided into two different sets based on covariates of colonization and extinction. The first set (directional dynamic) used only whether climate change pushed a site toward or away from the climatic niche centroid (represented by a binary variable, Δ). The second set (relative dynamic) used a relative distance index, δ, to examine how climate pushed a site relative to its starting and ending proximity to the climatic niche centroid. We defined:

$$\delta_\mathrm{T} = e^{\left(\frac{-|\mathbf{m}_\mathrm{T}|}{|\mathbf{h}_\mathrm{T}|}\right)} \text{ and } \delta_\mathrm{P} = e^{\left(\frac{-|\mathbf{m}_\mathrm{P}|}{|\mathbf{h}_\mathrm{P}|}\right)}$$

where $\mathbf{m}_\mathrm{T}$ and $\mathbf{m}_\mathrm{P}$ are the temperature and precipitation components of the vector from the modern climate at a site to the niche centroid (Fig. 2c). This index, δ, approaches zero when a site is located very close to the climatic niche centroid and then is moved by climate change very far away. It approaches 1 when a site is located far away from the climatic niche and is moved by climate change to the centroid of the niche. A site that does not change distance (i.e., no climate change) from the niche mean would have a value of δ equal to 0.37 (e^{-1}). We tested five different types of relative dynamic models (Table 2): a full model where δ_T and δ_P were covariates of both γ and ε, and the four possible combinations of either δ_T or δ_P as single covariates of γ and ε.

All eight occupancy models were compared and ranked by AIC weight, which gives an estimate of the weight of evidence from the data in support of a particular model (Burnham and Anderson 2002). To compare directly among hypotheses, the AIC weight of each model in the model set was calculated. The cumulative weight for all dynamic models (Burnham and Anderson 2002) was compared to the static and random models.

Results

Niche tracking was the overwhelming response of birds to climate change in our analysis. Of 53 focal bird species, 91% tracked either temperature or precipitation over time, and 26% of species tracked both temperature and precipitation (Table 1, Table S1). Species tracked precipitation toward wetter conditions, but tracked temperature toward cooler or warmer conditions, depending on the species (Fig. S1a-b).

We next examined the degree to which major climatological factors limiting species' historical distributions also explained distributional changes over time. Some species showed niche sensitivity (inferred from MaxEnt models; see Methods) for both environmental parameters and others for only one. Across all species, for each environmental parameter showing niche sensitivity, we tested for agreement between predicted sensitivity and observed tracking. For these cases (n=57), we found that 77% of *a priori* predictions of gradient sensitivity agreed with observed range shifts; excluding the five species that showed no niche tracking, this agreement increased to 85% (Table 1). Overall, *a priori* climatological sensitivities inferred from range-wide modeling were significantly associated with observed gradient tracking for both temperature (Fisher's exact test, 2-tailed: $P < 0.001$) and precipitation (Fisher's exact test, 2-tailed: $P = 0.049$).

Both the *a priori* predictions of gradient sensitivity and the observed environmental factors tracked by each species were significantly related to the average elevation occupied by a species (sensitivity: $F_{2,50} = 75.0$, $P < 0.001$; observations: $F_{3,49} = 20.4$, $P < 0.001$; data in Tables 1 and S1). Species tracking only precipitation were centered at an average elevation of 916 m (95% CI: 726 – 1,107 m), while species tracking only temperature were centered at an average elevation of 1,944 m (95% CI: 1,701 – 2,186 m). Similarly, species with western U.S. distributions sensitive to only precipitation were centered at an average elevation of 799 m (95% CI: 668 – 932 m), compared to an average elevation of 1,904 (95% CI: 1,774 – 2,033 m) for species sensitive to only temperature. Species sensitive to or tracking both precipitation and temperature were centered at intermediate elevations (95% CI for sensitivity: 609 – 1,257 m; 95% CI for tracking: 1,374 – 1,841 m). We also observed a similar pattern showing high correlation ($r = 0.923$) between elevational centers of species and climatic factors limiting NPP (Table S1). Low elevation species tended to occupy sites where NPP was limited by precipitation, high elevation species where NPP was limited by temperature, and middle elevation species where it was shaped by a combination of both climate variables. This suggests niche tracking may be governed by climate-induced shifts in NPP.

Site-specific models of colonization-extinction that incorporated niche components had greater AIC weights than the null model for 50 of 53 species (Table S2). For individual species, occupancy dynamics at the site were generally best explained by static or dynamic models (e.g., Figure S1c-f). Averaged across all species, the null model had 0.035 model weight, compared to 0.49 for the static model, and 0.47 cumulatively for dynamic models (Table 2). Comparing the different models that incorporate the niche, a dynamic model had a greater AIC weight than the static model for 53% of species, suggesting a mixed response for dynamic versus static models. Within the class of dynamic models, we compared results from five different parameterizations (see Methods and Table 2). Of these, the directional parameterization showed generally greater support (0.18 average model weight) than any other individual dynamic parameterization. Extinction probabilities were higher (0.264 ± 0.027, mean ± s.e.) across all species than colonization probabilities (0.131 ± 0.017; Table S2), when estimated from null models with fixed probabilities of colonization and extinction for all sites.

Discussion

For highly vagile species, like birds, the climatic niche can be a strong driver of responses to climate change. Our tests of niche tracking over the past 100 years showed that 48 of 53 bird species adjusted their geographic range as climate changed to move closer to their historically defined niche centroid for at least one environmental gradient (Table 1 and Table S1). Furthermore, there was strong agreement between the precipitation and temperature axes that species tracked and *a priori* predictions of which axes contribute most strongly to defining a species' climatic niche (Table 1 and Table S1).

Our results support the use of climatic niche modeling to predict future ranges of birds as a result of climate change (Araújo et al. 2005, Wiens and Graham 2005, Kearney 2006). The models assume that factors limiting a species' range may also drive temporal changes to its distribution. Our results provide evidence in support of this assumption, adding to a small but growing body of evidence based on tests within native ranges across time (Martinez-Meyer et al. 2004, Araújo et al. 2005, Martinez-Meyer and Peterson 2006, Monahan and Hijmans 2008).

Bird species exhibited individualistic but generally predictable responses to temperature or precipitation shifts. This suggests that the highly individualistic responses of species to past and present climate change (Taper et al. 1995, Brown et al. 1996, Moritz et al. 2008) may be explained by differing species-specific sensitivities to climatic parameters (Davis et al. 1998b, Araújo et al. 2006) and the direction of climate change relative to the climatic niche. Climate change may push some sites or populations closer to the centroid of their climatic niche, and other sites or populations farther away. Species might also respond more to precipitation or changes in environmental extremes than to changes in average temperature. Thus, not all species or populations should be expected to move upward in elevation or poleward in latitude (Peters and Darling 1985, Parmesan and Yohe 2003) as they respond in climate space to a shifting environment; instead, a great diversity of geographic responses should not only be predicted (Peterson et al. 2002), but expected, especially in topographically complex environments (Parra and Monahan 2008).

All five species that did not track their climatic niche for either environmental factor (Nuttall's Woodpecker, California Thrasher, Anna's Hummingbird, Black Phoebe, and Western Scrub-Jay) inhabit low elevations and can easily exploit human-dominated areas such as urban, suburban, and agricultural ecosystems (Blair 1996). In comparison, four species found in similar elevational ranges (Table S1) that avoid human-dominated areas tracked at least one environmental variable, although some species that exploit urban areas did show niche tracking (e.g., Oak Titmouse and California Towhee). The apparent association with urbanization of species that did not track their climatic niche may have implications for conservation. Species that have colonized urban, suburban, and agricultural ecosystems may be able to expand or sustain a range far from their climatic niche (either through access to key resources or use of uniquely human microclimates) and thereby escape the negative consequences of climate change.

Occupancy dynamics are the unseen mechanism behind range changes (Brown et al. 1996, Holt et al. 2005, Anderson et al. 2009). Incorporating the climatic niche into our models of occupancy dynamics between two time periods resulted in mixed conclusions: niche-centric models of occupancy (i.e., static and dynamic models; Fig. 3) explained transitions of site occupancy better than the null model, but evidence was equivocal as to whether climate change strongly impacted these transitions. This outcome could result from using climatic variables in defining the fundamental niche that were less important than other unexamined variables. For example, our results indicate that focal bird species may have tracked changes in temperature and precipitation through their combined influences on annual NPP, a variable implicated in a similar response to climate change in eastern North America (Monahan and Hijmans 2008). The importance of NPP could indicate that factors affecting energy availability are shaping range limits rather than, or in addition to, physiological tolerances to climatic extremes.

The role of climate change in shaping site turnover dynamics should be considered in relation to the relative magnitude of climatic shift (Fig. 2c). If climate change shifts sites in environmental space only a small amount relative to their distance from the niche centroid, then we may not expect to detect a strong signal of dynamic niche tracking. As climate change continues to shift environmental conditions of sites, more species may be likely to exhibit site turnovers leading to range change. This may be especially true, given that the magnitude of expected climate change by 2100 appears likely to exceed the observed change in the preceding century (IPCC 2007). Our analyses indicate that niche tracking appears widespread – albeit variable – in birds, and may be the guiding principle through which we expect to see other species respond.

Table 1. Predicted climatic sensitivities for 53 bird species and the observed climate variables that species were found to track.

	Observed Tracking			
Predicted Tracking[*]	Temperature	Precipitation	Both	Neither
Temperature	**12**	4	**9**	–
Precipitation	1	**14**	**4**	5
Both	–	3	**1**	–

*Predicted climatic sensitivities based on relative support of climatic variables from MaxEnt models to explain whole range distributions of species (see Methods and Table S1). Bolded cells indicate comparisons where observed response matched the predicted response.

Table 2. Average strength of evidence for multiple hypotheses of site-specific niche-tracking

Model	Parameterizations of colonization (γ) and extinction (ε)[*]	Number of parameters[†]	Average AIC weight[‡]
Null	$\text{logit}(\gamma) = \beta_0$ $\text{logit}(\varepsilon) = \beta_1$	4	0.035
Static	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \mathbf{h}_\text{T} + \beta_2 \cdot \mathbf{h}_\text{P}$ $\text{logit}(\varepsilon) = \beta_3 + \beta_4 \cdot \mathbf{h}_\text{T} + \beta_5 \cdot \mathbf{h}_\text{P}$	8	0.492
Dynamic[§]	-	-	0.473
Directional[¶]	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \Delta_\text{T} + \beta_2 \cdot \Delta_\text{P}$ $\text{logit}(\varepsilon) = \beta_3 + \beta_4 \cdot \Delta_\text{T} + \beta_5 \cdot \Delta_\text{P}$	8	0.177
Full relative	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \delta_\text{T} + \beta_2 \cdot \delta_\text{P}$ $\text{logit}(\varepsilon) = \beta_3 + \beta_4 \cdot \delta_\text{T} + \beta_5 \cdot \delta_\text{P}$	8	0.087
Precipitation-only	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \delta_\text{P}$ $\text{logit}(\varepsilon) = \beta_2 + \beta_3 \cdot \delta_\text{P}$	6	0.062
Temperature-only	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \delta_\text{T}$ $\text{logit}(\varepsilon) = \beta_2 + \beta_3 \cdot \delta_\text{T}$	6	0.058
Hybrid 1	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \delta_\text{P}$ $\text{logit}(\varepsilon) = \beta_2 + \beta_3 \cdot \delta_\text{T}$	6	0.045
Hybrid 2	$\text{logit}(\gamma) = \beta_0 + \beta_1 \cdot \delta_\text{T}$ $\text{logit}(\varepsilon) = \beta_2 + \beta_3 \cdot \delta_\text{P}$	6	0.044

[*] Occupancy models also include detectability (*p*) and occupancy (ψ_0). See Methods for details on these parameters, as well as definitions of variables.

[†] Number of parameters is based on constant detectability and occupancy models.

[‡] Weights are averaged across results from 53 species.

[§] AIC weight given as the sum of the weights of the following 6 dynamic models.

[¶] The binary variable Δ is given the value of 1 when the site is moving toward the niche center on an environmental axis, and 0 when the site is moving away from the niche center.

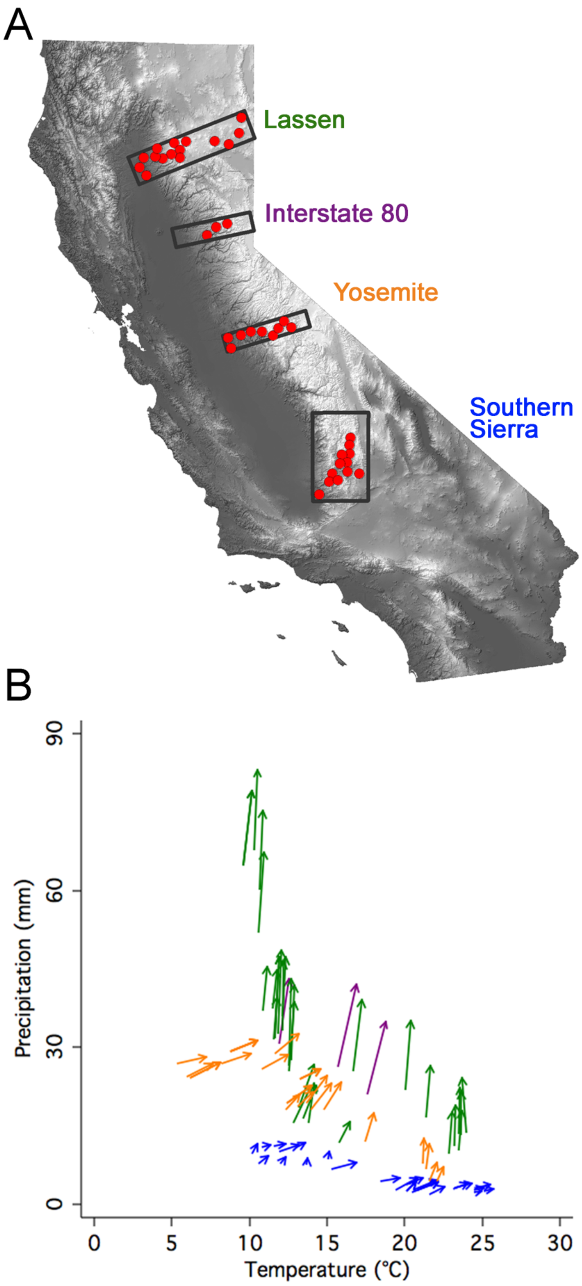


Figure 1. Locations of 82 bird survey sites in both geographical and climatic space. (a) Geographical locations of cross-sectional resurvey transects through the Sierra Nevada superimposed onto topography of California (higher elevations in lighter gray). Locations of neighboring survey sites (red circles) have been aggregated to provide visual clarity. The number of sites per transect from south to north are: Southern Sierra (25); Yosemite (24); Interstate 80 (3); and Lassen (30). (b) Locations of resurvey sites in climate space, with arrows pointing from historical breeding season climate to modern breeding season climate. Color-codes correspond to transect: Southern Sierra in blue, Yosemite in orange, Interstate 80 in purple, and Lassen in green.

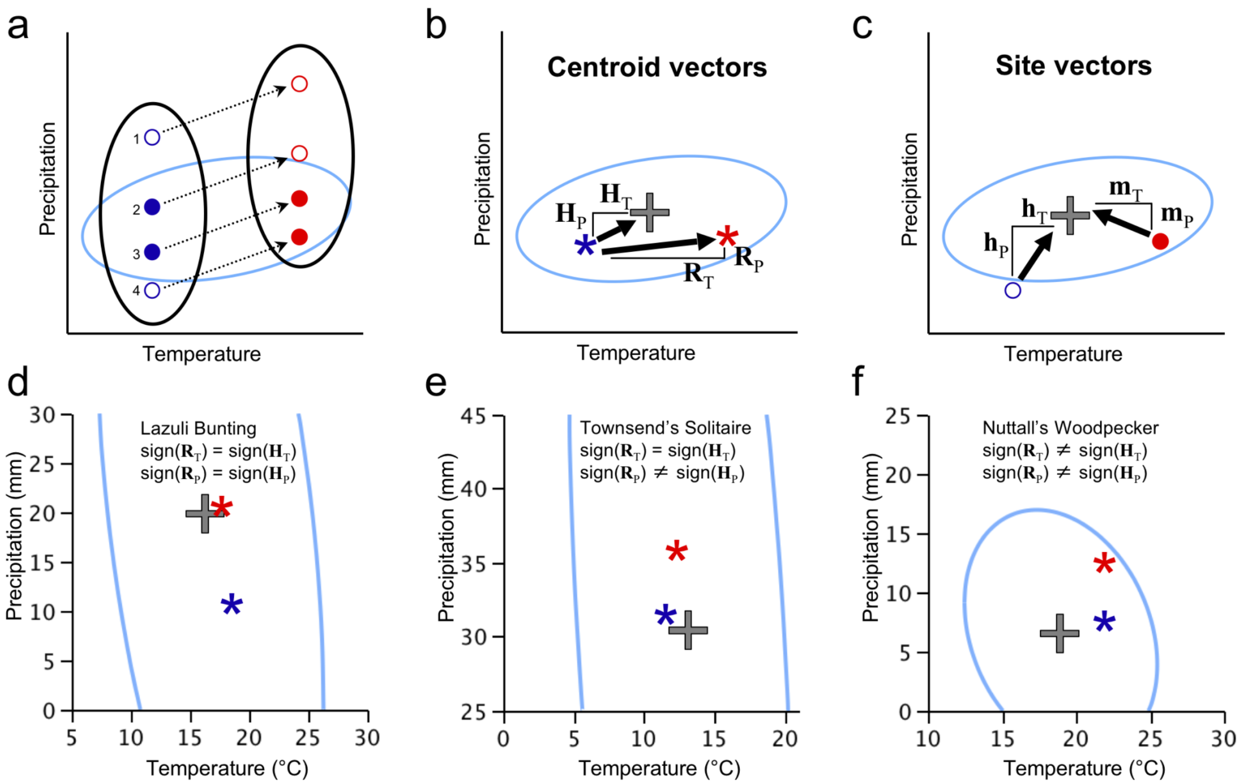


Figure 2. Colonization-extinction dynamics as mediated by shifting climates lead to changes in position of occupied range centroids relative to the climatic niche. (a) Four sites (circles labeled 1-4) within a geographic area (black ellipse) experience shifts in climate over time (dotted arrows), moving sites from a prior climatic position (blue circles) to a current climatic position (red circles). For a hypothetical species with a certain climatic niche defined by temperature and precipitation (light blue ellipse), a site can be unoccupied in both time periods if it remains outside the climatic niche (Site 1), go extinct if the site shifts out of the climatic niche (Site 2), stay occupied in both time periods if it remains inside the climatic niche (Site 3), or be colonized if the site enters the climatic niche (Site 4). (b) The centroids of the observed occupied ranges for a species in each time period (asterisks: blue for historic and red for current) can provide evidence of niche tracking when compared to the centroid of a species' climatic niche (gray cross). If the temperature or precipitation components of the vector from the historic range centroid to the climatic niche centroid ($\mathbf{H}_T$ and $\mathbf{H}_P$, respectively) agree in sign with the corresponding climatic components of the vector from the historic range centroid to the current range centroid ($\mathbf{R}_T$ and $\mathbf{R}_P$), then there is evidence for tracking for that component. (c) Individual sites can be defined by vector components describing the position of a site (e.g., site 4) either historically ($\mathbf{h}_T$ and $\mathbf{h}_P$) or currently ($\mathbf{m}_T$ and $\mathbf{m}_P$) relative to the climatic niche centroid. These site-specific vectors are used in combinations as covariates of colonization and extinction in occupancy models. Examples of movements of range centroids for three species show different levels of climatic niche tracking (for further details and other species, see Table S1). (d) Lazuli Bunting showed niche tracking of both temperature and precipitation, shifting to a cooler and wetter occupied range. The light blue circle is a 95% density ellipse around the full range of historic specimens that defined the climatic niche centroid. (e) Townsend's Solitaire showed

niche tracking of temperature, but not precipitation. (f) Nuttall's Woodpecker tracked neither temperature nor precipitation components of the climatic niche.

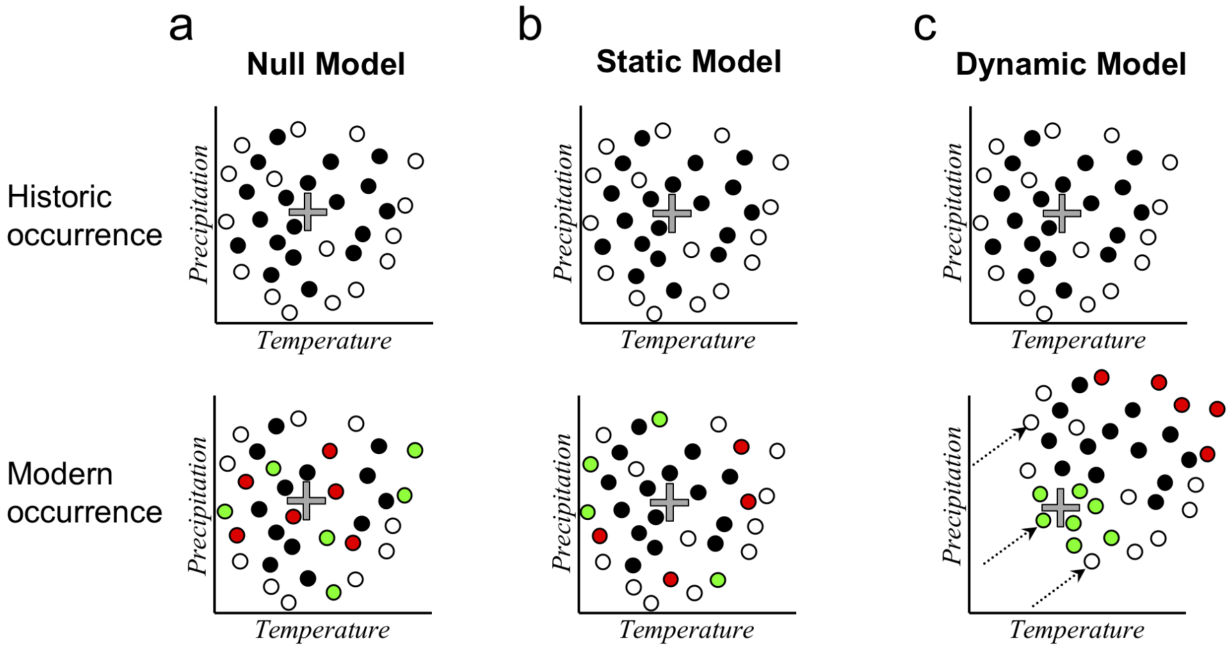


Figure 3. Models of site-specific change in occupancy in relation to the climatic niche. Sites are observed to be either occupied (black) or unoccupied (open), and between time periods they can either go extinct (red) or be colonized (green). (a) The null model estimates a constant probability of colonization and extinction; consequently, sites are equally likely to change occupancy status regardless of their proximity to the climatic niche centroid (gray cross). (b) The static model estimates turnover probabilities as a function of the distance from a site to the niche centroid, leading to changes in occupancy at the periphery of the climatic range. (c) The dynamic model (see Methods for six formulations) incorporates the degree to which sites have shifted in climate space over time (arrows). Thus, turnover probabilities are a function of the distance from a site to the niche centroid at present, relative to where it was in the past. This leads to a directional pattern in occupancy turnover.

Table S1. Climatological tracking of niche means by species, from low elevation species to high elevation species

Species		Average historical elevation (m)[*]	Suburban adaptable[†]	$\mathbf{R}_T$ (°C)[‡]	$\mathbf{H}_T$ (°C)[‡]	$\mathbf{R}_P$ (mm)	$\mathbf{H}_P$ (mm)	*A priori* sensitivity[§]	Observed climate tracking	NPP score[¶]
Nuttall's Woodpecker	*Picoides nuttallii*	451	yes	0.02	-2.96	5.04	-1.00	precip	none	1.00
Oak Titmouse	*Baeolophus inornatus*	547	yes	0.60	-2.42	4.80	0.77	precip	precip	1.00
Bullock's Oriole	*Icterus bullockii*	591	yes	0.00	-1.89	5.87	5.10	precip	precip	1.00
California Towhee	*Pipilo crissalis*	591	yes	1.12	-2.19	4.81	0.85	precip	precip	1.00
Acorn Woodpecker	*Melanerpes formicivorus*	594	yes	0.78	-1.76	4.87	3.19	precip	precip	1.00
Western Kingbird	*Tyrannus verticalis*	600	-	0.51	-2.31	5.36	12.36	precip	precip	1.00
California Quail	*Callipepla californica*	618	-	0.97	-2.59	3.85	0.16	precip	precip	1.00
California Thrasher	*Toxostoma redivivum*	631	yes	1.47	-1.64	3.39	-2.14	precip	none	1.00
Lark Sparrow	*Chondestes grammacus*	648	-	0.19	-2.44	2.30	12.76	precip	precip	0.96
Bewick's Wren	*Thryomanes bewickii*	689	yes	0.63	-1.60	4.79	5.97	precip	precip	0.94
Ash-throated Flycatcher	*Myiarchus cinerascens*	721	no	1.79	0.66	3.56	3.58	precip	temp, precip	1.00
Anna's Hummingbird	*Calypte anna*	730	yes	0.04	-1.79	5.14	-3.48	precip	none	1.00
Bushtit	*Psaltriparus minimus*	742	yes	0.36	-2.74	7.12	2.98	precip	precip	0.95
Western Meadowlark	*Sturnella neglecta*	750	-	1.16	-2.46	4.11	10.11	precip	precip	0.89
Black Phoebe	*Sayornis nigricans*	754	yes	0.96	-0.28	6.01	-0.20	precip	none	1.00
Wrentit	*Chamaea fasciata*	788	no	1.59	-1.61	3.07	1.28	temp	precip	1.00
Lawrence's Goldfinch	*Carduelis lawrencei*	803	-	0.06	-1.89	6.89	2.33	precip	precip	1.00
Western Bluebird	*Sialia mexicana*	809	yes	-0.14	-2.25	5.62	6.78	temp, precip	temp, precip	0.96
Violet-green Swallow	*Tachycineta thalassina*	872	yes	1.25	-1.04	4.81	0.63	temp, precip	precip	0.81
Lazuli Bunting	*Passerina amoena*	898	-	-1.19	-1.96	9.65	9.27	precip	temp, precip	0.91
Lesser Goldfinch	*Carduelis psaltria*	900	yes	0.60	-0.36	4.75	0.57	precip	precip	0.87
Western Scrub-Jay	*Aphelocoma californica*	921	yes	2.53	-1.26	2.25	-0.67	precip	none	0.96
Canyon Wren	*Catherpes mexicanus*	956	-	-0.28	1.80	8.96	6.90	precip	precip	0.93
Spotted Towhee	*Pipilo maculatus*	993	yes	0.54	-1.30	5.57	4.64	temp, precip	precip	0.89
Black-headed Grosbeak	*Pheucticus melanocephalus*	1003	-	1.19	-0.58	7.40	7.66	precip	precip	0.90
Pacific-slope Flycatcher	*Empidonax difficilis*	1052	yes	1.21	2.07	4.50	-3.10	precip	temp	0.86
Brewer's Blackbird	*Euphagus cyanocephalus*	1060	yes	0.39	-0.49	7.56	2.40	temp, precip	precip	0.83
Cassin's Vireo	*Vireo cassinii*	1249	-	-1.55	-0.53	11.61	1.11	temp	temp, precip	0.76
Black-throated Gray Warbler	*Dendroica nigrescens*	1395	-	1.65	1.27	8.26	0.87	precip	temp, precip	0.78
"Red-shafted" Northern Flicker	*Colaptes auratus cafer*	1501	-	1.16	0.07	5.47	17.54	temp	temp, precip	0.64

Rock Wren	*Salpinctes obsoletus*	1573	-	1.41	1.37	5.75	-1.09	temp	temp	0.56
Western Wood-Pewee	*Contopus sordidulus*	1593	no	1.69	2.34	5.43	0.45	precip	temp, precip	0.62
Hermit Warbler	*Dendroica occidentalis*	1613	-	0.16	-0.70	14.44	4.52	temp	precip	0.63
Western Tanager	*Piranga ludoviciana*	1618	-	2.87	0.51	0.81	2.76	temp	temp, precip	0.53
MacGillivray's Warbler	*Oporornis tolmiei*	1653	-	0.47	0.05	5.35	5.47	temp	temp, precip	0.43
Calliope Hummingbird	*Stellula calliope*	1785	-	-0.40	0.48	6.98	2.56	temp	precip	0.53
Mountain Quail	*Oreortyx pictus*	1859	-	1.49	1.85	9.27	-5.33	temp	temp	0.61
Dusky Flycatcher	*Empidonax oberholseri*	1870	-	0.29	1.56	7.03	-3.40	temp	temp	0.42
Steller's Jay	*Cyanocitta stelleri*	1878	no	0.83	2.30	7.54	-3.29	temp	temp	0.45
Red-breasted Sapsucker	*Sphyrapicus ruber*	1880	-	0.10	0.50	13.60	-1.30	temp	temp	0.61
White-headed Woodpecker	*Picoides albolarvatus*	1976	-	0.82	1.68	8.59	-3.74	temp	temp	0.55
Green-tailed Towhee	*Pipilo chlorurus*	2043	-	0.94	1.90	4.92	-1.56	temp	temp	0.52
White-crowned Sparrow	*Zonotrichia leucophrys*	2053	-	-4.67	-0.53	4.16	6.79	temp	temp, precip	0.53
Mountain Chickadee	*Poecile gambeli*	2063	-	0.85	1.36	6.77	-3.38	temp	temp	0.39
"Audubon's" Yellow-rumped Warbler	*Dendroica coronata auduboni*	2064	-	0.96	1.48	7.21	0.56	temp	temp, precip	0.43
Townsend's Solitaire	*Myadestes townsendi*	2084	-	0.80	1.46	4.37	-1.02	temp	temp	0.17
Pygmy Nuthatch	*Sitta pygmaea*	2101	-	-0.05	1.57	14.39	7.52	temp	precip	0.82
Hammond's Flycatcher	*Empidonax hammondii*	2102	-	1.53	3.11	11.49	1.06	temp	temp, precip	0.36
Cassin's Finch	*Carpodacus cassinii*	2161	-	0.86	1.01	3.93	-5.12	temp	temp	0.17
American Dipper	*Cinclus mexicanus*	2308	-	1.23	1.64	11.71	-4.58	temp	temp	0.36
Williamson's Sapsucker	*Sphyrapicus thyroideus*	2404	-	0.91	0.22	5.45	7.34	temp	temp, precip	0.45
Mountain Bluebird	*Sialia currucoides*	2447	-	0.30	1.33	8.11	4.99	temp	temp, precip	0.53
Clark's Nutcracker	*Nucifraga columbiana*	2519	-	1.44	0.38	1.24	-3.33	temp	temp	0.29

[*] Estimated as the average elevation a species was observed historically, weighted by the number of occasions a species was seen at a site.

[†] Based on classifications from Blair (1996).

[‡] The vectors $\mathbf{H}_T$, $\mathbf{H}_P$, $\mathbf{R}_T$, and $\mathbf{H}_P$ define climatic distances between the observed historical range mean and the niche centroid ($\mathbf{H}_t$, $\mathbf{H}_p$) and between the historical observed range mean and the modern observed range mean ($\mathbf{R}_T$, $\mathbf{R}_P$).

[§] Predicted climatic sensitivities based on relative support of climatic variables to explain whole-range distributions of species, as modeled in MaxEnt.

[¶] NPP score is calculated as the proportion of sites in a species' observed range where precipitation (versus temperature) is the limiting factor of net primary productivity (see Methods).

Table S2. Model weights of multiple hypotheses for site-specific niche-tracking.

Species	Detectability Model	AIC Model weights (w_i)*								Estimated parameters†		
				Dynamic								
		Null (random)	Static	Directional	Full Relative	Temperature-only	Precipitation-only	Hybrid 1	Hybrid 2	ψ_0	γ	ε
Acorn Woodpecker	era, jday	0.00	**0.39**	0.00	0.06	0.30	0.00	0.00	0.25	0.265	0.051	0.221
American Dipper	era, jday	0.01	0.07	0.01	0.28	0.00	0.31	**0.31**	0.00	0.301	0.054	0.858
Anna's Hummingbird	era, jday	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.130	0.482	0.239
Ash-throated Flycatcher	era, jday	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.393	0.097	0.198
Bewick's Wren	.	0.00	**0.90**	0.10	0.00	0.00	0.00	0.00	0.00	0.256	0.229	0.181
Black Phoebe	.	0.00	0.34	**0.65**	0.00	0.00	0.00	0.00	0.00	0.438	0.143	0.415
Black-headed Grosbeak	.	0.01	**0.97**	0.01	0.00	0.00	0.00	0.00	0.00	0.482	0.199	0.198
Black-throated Gray Warbler	.	**0.33**	0.05	0.05	0.04	0.07	0.20	0.08	0.16	0.325	0.026	0.463
Brewer's Blackbird	era	0.03	**0.88**	0.01	0.01	0.02	0.02	0.02	0.02	0.477	0.416	0.154
Bullock's Oriole	.	0.00	**0.97**	0.03	0.00	0.00	0.00	0.00	0.00	0.317	0.213	0.037
Bushtit	.	0.02	0.09	**0.65**	0.03	0.01	0.10	0.10	0.01	0.392	0.044	0.141
California Quail	era, jday	0.00	0.28	**0.72**	0.00	0.00	0.00	0.00	0.00	0.321	0.046	0.057
California Thrasher	.	0.03	0.00	0.37	**0.48**	0.02	0.04	0.05	0.01	0.101	0.021	0.397
California Towhee	era	**0.41**	0.04	0.26	0.01	0.06	0.08	0.06	0.08	0.325	0.000	0.192
Calliope Hummingbird	.	0.02	0.04	**0.32**	0.07	0.26	0.00	0.01	0.28	0.317	0.231	0.376
Canyon Wren	era	0.08	0.03	0.05	**0.53**	0.21	0.01	0.08	0.02	0.279	0.023	0.570
Cassin's Finch	.	0.00	0.19	**0.81**	0.00	0.00	0.00	0.00	0.00	0.417	0.176	0.101
Cassin's Vireo	era, jday	0.00	0.35	**0.62**	0.01	0.00	0.01	0.00	0.02	0.531	0.166	0.290
Clark's Nutcracker	era	0.00	**0.96**	0.00	0.03	0.00	0.00	0.00	0.00	0.415	0.024	0.268
Dusky Flycatcher	era	0.00	0.00	0.13	0.09	**0.52**	0.00	0.00	0.26	0.311	0.316	0.154
Green-tailed Towhee	.	0.02	0.07	0.00	0.07	**0.50**	0.00	0.00	0.33	0.426	0.025	0.405
Hammond's Flycatcher	era, jday	0.00	**0.99**	0.00	0.00	0.00	0.00	0.00	0.00	0.208	0.058	0.400
Hermit Warbler	.	0.00	**0.97**	0.03	0.00	0.00	0.00	0.00	0.00	0.358	0.152	0.317
Lark Sparrow	era, jday	0.00	0.00	0.32	**0.64**	0.03	0.00	0.01	0.01	0.360	0.135	0.479
Lawrence's Goldfinch	.	0.00	**0.99**	0.01	0.00	0.00	0.00	0.00	0.00	0.215	0.173	0.197
Lazuli Bunting	.	0.02	0.00	0.10	0.11	0.00	**0.62**	0.10	0.05	0.350	0.249	0.543
Lesser Goldfinch	era	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.446	0.179	0.175
MacGillivray's Warbler	era	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.413	0.155	0.233
Mountain Bluebird	.	0.00	0.00	0.00	0.12	0.32	0.00	**0.55**	0.00	0.231	0.099	0.665
Mountain Chickadee	.	0.00	0.17	0.01	**0.66**	0.00	0.02	0.00	0.14	0.622	0.000	0.018

Mountain Quail	era, jday	0.01	0.16	0.30	0.02	0.01	0.17	0.02	**0.31**	0.415	0.106	0.192
"Red-shafted" Northern Flicker	.	0.01	0.10	0.02	0.13	0.02	**0.48**	0.20	0.05	0.893	0.000	0.107
Nuttall's Woodpecker	.	0.00	**0.68**	0.02	0.23	0.02	0.01	0.01	0.02	0.226	0.042	0.084
Oak Titmouse	era, jday	0.01	**0.75**	0.14	0.02	0.00	0.04	0.04	0.00	0.260	0.014	0.014
Pacific-slope Flycatcher	era	0.19	0.03	0.03	0.02	0.12	**0.23**	0.15	0.23	0.145	0.007	0.118
Pygmy Nuthatch	.	0.01	**0.96**	0.01	0.00	0.00	0.01	0.00	0.01	0.164	0.063	0.679
Red-breasted Sapsucker	.	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.280	0.232	0.187
Rock Wren	.	**0.38**	0.21	0.01	0.03	0.13	0.06	0.14	0.06	0.441	0.046	0.508
Spotted Towhee	era	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.408	0.183	0.106
Steller's Jay	.	0.00	0.07	0.14	**0.72**	0.00	0.03	0.03	0.00	0.581	0.133	0.035
Townsend's Solitaire	era, jday	0.00	0.08	0.00	0.39	**0.47**	0.00	0.00	0.06	0.350	0.159	0.052
Violet-green Swallow	era, jday	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.390	0.164	0.446
Western Bluebird	.	0.08	**0.35**	0.14	0.03	0.02	0.18	0.18	0.02	0.399	0.111	0.388
Western Kingbird	era, jday	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.371	0.042	0.126
Western Meadowlark	.	0.00	0.00	**0.95**	0.02	0.00	0.01	0.00	0.01	0.423	0.020	0.366
Western Scrub-Jay	era, jday	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.399	0.094	0.189
Western Tanager	.	0.20	**0.55**	0.11	0.01	0.04	0.03	0.03	0.04	0.536	0.431	0.026
Western Wood-Pewee	era, jday	0.22	0.04	0.05	0.07	0.20	0.06	**0.33**	0.04	0.682	0.577	0.130
White-crowned Sparrow	.	0.00	**0.99**	0.01	0.00	0.00	0.00	0.00	0.00	0.311	0.000	0.709
White-headed Woodpecker	era, jday	0.00	**0.99**	0.00	0.00	0.00	0.00	0.00	0.00	0.332	0.103	0.099
Williamson's Sapsucker	.	0.00	**0.92**	0.00	0.06	0.01	0.00	0.00	0.00	0.185	0.089	0.200
Wrentit	era, jday	0.00	0.08	**0.34**	0.13	0.22	0.00	0.00	0.22	0.168	0.047	0.240
"Audubon's" Yellow-rumped Warbler	.	0.00	0.00	0.05	0.14	0.00	**0.72**	0.08	0.00	0.634	0.110	0.048

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[*] Model weights in bold signify top-ranked models. Parameterization of models is provided in Table 2.

[†] Parameter estimates for initial probability of occupancy (ψ_0), colonization (γ), and extinction (ε) are based on the null model, providing constant probabilities.

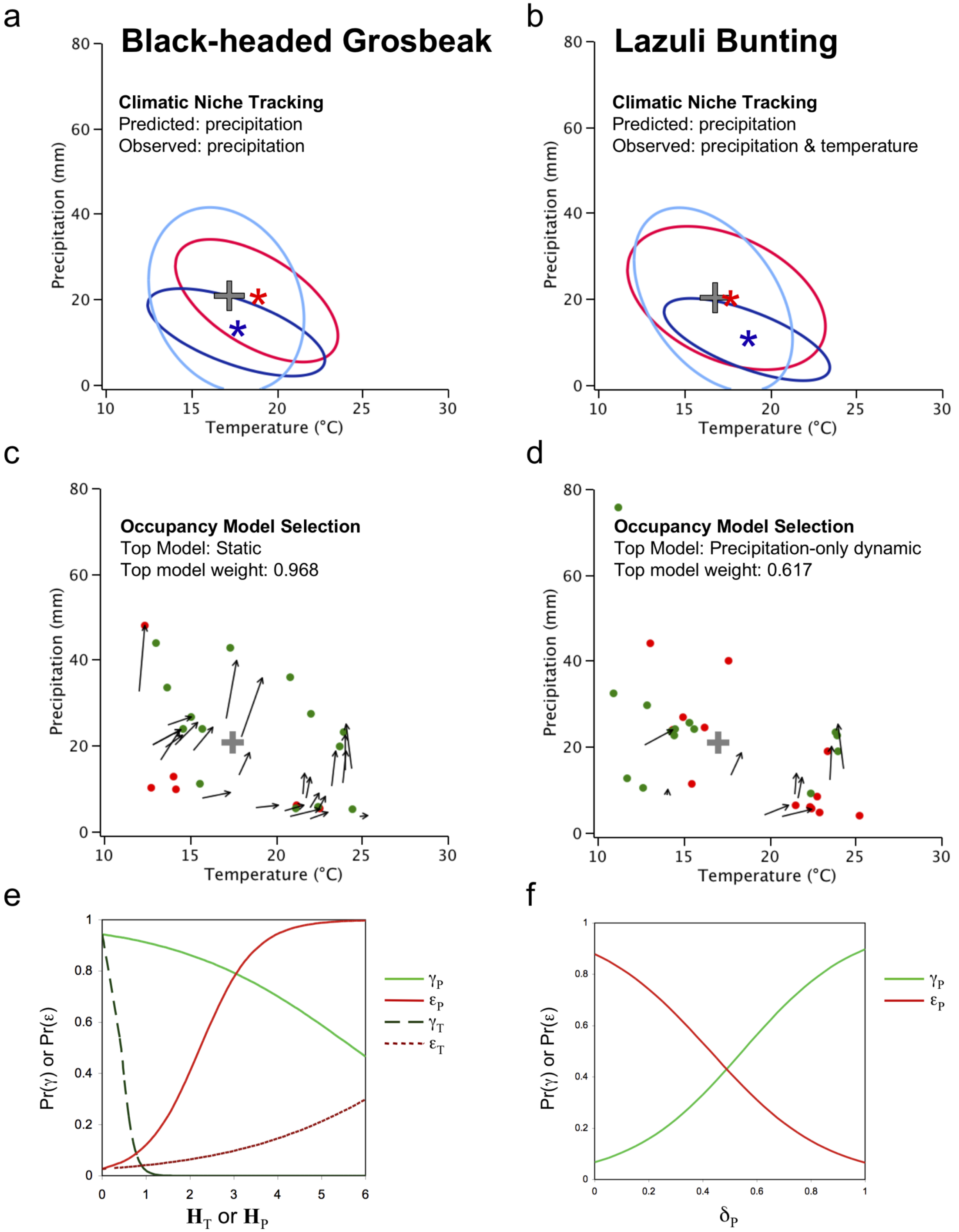


Figure S1. Graphical examples of niche tracking, occupancy changes, and modeled parameters for two species, Black-headed Grosbeak (a, c, e) and Lazuli Bunting (b, d, f). Historical (blue dot) and modern (red dot) observed range means for each species (a, b) shift over time, relative to each species' climatic niche (gray cross). Variability is represented by 50% density ellipses around means (light blue for niche, dark blue for historic, red for current). Site-specific occupancy dynamics over time (c, d) can be described by three categories: sites that went extinct (red dots), sites that became colonized (green dots), and sites that stayed occupied through time (black arrows), thereby moving from historical climate to modern climate. Modeled colonization (γ) and extinction (ε) parameters are shown as functions of top occupancy model variables (e, f). For the black-headed grosbeak (e), the distance from a site to the climatic niche (static model) explained the data best. For the lazuli bunting (f), a precipitation-only dynamic model showed that if a site was close to the climatic niche centroid in precipitation and was moved far away by climate change ($\delta \rightarrow 0$) then that site would have low colonization and high extinction probabilities.

Chapter 3.

Temperature alone does not explain patterns of avian elevational range change

Abstract

As global climate warms, species are expected to track climates poleward in latitude and uphill in elevation. Empirical studies largely support this pattern but have seldom looked closely at species that shift in other directions or not at all, and the factors, climatic or otherwise, that drive this variability. We resurveyed bird communities along three elevational transects of the Sierra Nevada mountains of California originally visited 80-100 years ago, allowing us to test for elevational shifts in both range centers and range limits using statistical techniques to account for false absences and provide unbiased estimates of species occurrence. As expected with average warming over the region, we detected species shifting upward, but this pattern only described 56% of shifts for 99 species. Considering changes in both temperature and precipitation at occupied sites increased the proportion of shifts explained to 82%. Species that had low clutch size, were highly territorial, and were year-round US residents were significantly more likely to shift elevational ranges than other species. Our results illustrate the complex interplay between species-specific and region-specific factors that structure patterns of range change over long time periods.

Introduction

Global climate change is expected to shift the distributions of organisms around the world, with predicted consequences of massive range retractions (Thomas et al. 2004), creation of ‘no-analogue’ communities (Roy et al. 1996, Williams 2007, Stralberg et al. 2009), and alarming rates of mountaintop and tropical extinctions (La Sorte and Jetz 2010, Sinervo et al. 2010). Species moving “up” – in both latitude and elevation – are the “fingerprints” of climate change impacts, and have been observed in numerous local, long-term studies of plants and animals (Parmesan and Yohe 2003, Root et al. 2003, Moritz et al. 2008). However, these studies have found a much wider variety of responses to climate change than the simple rule of species moving up; between 20-25% of species have shifted ranges downslope or latitudinally south, and an additional 10-30% of species have not shifted their range (Parmesan and Yohe 2003). A limited understanding of the complexities underlying these variable, 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 non-temperature environmental gradients (Tingley et al. 2009, Zimmermann et al. 2009, Crimmins et al. 2011), and stochastic fluctuations in population size (Lenoir et al. 2010). Non-movement, or range stability, may result from adaptation of local populations to new climates (Rodríguez-Trelles and Rodríguez 1998, Parmesan et al. 2005), an inability to disperse (Davis et al. 1998a), a failure for climate to have shifted enough 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 held by diverse species assemblages. Past studies have had moderate success at linking 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). However, in most cases the statistical power to determine these relationships is greatly limited (Angert et al. in review), and results may be obscured by the effects of false absences on occurrence data (Link and Nichols 1994, Kery 2004, Kery et al. 2006, Hochachka and Fiedler 2008). Given the multitude of mechanisms and processes potentially driving range change, temporally and spatially replicated surveys across taxa are necessary to differentiate support for these hypotheses (Parmesan et al. 2005).

We present results of a 6-year resurvey of birds based on systematic observations originally collected between 80 and 100 years ago along elevational gradients in the Sierra Nevada mountains of California, U.S.A. The historical and modern data consist of sites repeatedly visited by trained observers that allow us to account for false absences in occurrence data through estimation of species-, survey- and era-specific probabilities of detection. Surveys were conducted in three different regions of the Sierra Nevada spanning over 5° of latitude (Figure 1). Comparisons across regions allow us to estimate geographic variability in range shifts both among- and within-species.

Although climate has warmed on average throughout the Sierra Nevada over the last century (Bonfils et al. 2008b), there is a large degree of heterogeneity in both temperature and precipitation records (Figure 2a-c). With warmer temperatures, species are expected to track climates to higher elevations (Parmesan and Yohe 2003), yet this only holds true if temperature change is constant and positive across the elevational gradient. Warming has occurred substantially in the southern and central Sierra Nevada over the last 100 years, but the northern Sierra Nevada has warmed only marginally, including some evidence of local cooling (Figure 2a). Moreover, precipitation typically increases with elevation, and precipitation has generally increased over the same time period (especially in the north, Figure 2a). If species track precipitation instead of temperature (Tingley et al. 2009, Crimmins et al. 2011), this could explain some downward shifts in elevation. To consider this hypothesis, we measured the difference in elevation between each survey site and its closest regional modern climatic neighbor (Figure 2d-f, see Methods and Figures S1 and S2 for more information). Given the average warming trend, the majority of sites have modern nearest temperature neighbors at higher elevations, but with more varied precipitation trends, some sites have modern nearest precipitation neighbors over 1500 m lower. Consequently, in many parts of the Sierra Nevada, temperature and precipitation changes over the past century yield opposite expectations as to whether species should be moving up or down. Given this knowledge, our goals were to: (1) test for an overall signal in upward shifting 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. While we expect climate to cause species to shift their elevational ranges (up or down depending on climatic sensitivity), why certain species do not move is unclear. Based on previous studies (Pounds et al. 1999, Moritz et al. 2008), low elevation species should respond differently from high elevation species, particularly with regards to shifts at range limits. Additionally, we hypothesized that dispersal- and colonization-related traits should be positively related to range movements (Angert et al. in review), including migration during the non-breeding season, large clutch size, large home range size, small body size, low territoriality, and a generalist diet.

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 multi-year 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, consisting of a nothern cross-section through Lassen Volcanic National Park, a central cross-section through Yosemite National Park, and a southern cross-section through the Kern Plateau and a section of Sequoia National Park (Figure 1). 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 – 2,751 m for northern sites, 65 – 3,226 for central sites, and 61 – 3,356 m for southern sites.

Historical bird observations were conducted between 1911 and 1929 as part of regular surveys by Joseph Grinnell, Tracy Storer, and seven other researchers from the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (Grinnell and Storer 1924, Grinnell et al. 1930). Surveys were taken opportunistically using the line-transect method (Bibby et al. 2000). While information on absolute abundance of species varied, surveys uniformly listed each species encountered, providing reliable detection/non-detection data. All survey observations, as well as details on location, extent, duration, and weather, were recorded in field notebooks held at the MVZ (and 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 site surveyed a total of 1 – 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, transects were placed following named geographical features in habitats similar to those described in the field notes. Birds were surveyed using variable-distance point counts (Ralph et al. 1995) lasting 7 minutes. Observation points were separated by a minimum of 250 m. The total number of points per line-transect varied depending on the extent of the historical route (median = 10 points over 2.5 km). Six trained primary observers collected data as part of 1 or 2-person survey teams between 2003 and 2009. A total of 251 modern surveys were conducted at 84 sites, with each site surveyed a maximum of 5 times (median = 3).

Bird surveys characterized breeding communities. Historically, survey dates ranged between March 25th and October 2nd, with 77% conducted between May 1st and July 31st. There was a strong relationship between date of survey and elevation; low elevation areas were surveyed early in the spring and high elevation areas were surveyed later in the summer when mountain passes became accessible. Modern resurveys visited sites around the same time as historical surveys, but were concentrated within the breeding season (dates ranged between May 3rd and August 25th). As both migrating birds and post-breeding 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, with 163 species detected at least once in both eras. Since not all species occurred across all three survey regions, we created independent lists for each region of species detected at a minimum of 10% of sites within each era. We additionally excluded all non-passerines, since most were observed sporadically, except those in five families: Odontophoridae, Phasianidae, Columbidae, Trochilidae, and Picidae. Our final regional species list tallied 78 species for northern, 78 species for central, and 73 species for southern regions. Combining the three regions results 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, MacKenzie et al. 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 and Beissinger 2009), which tests for a temporal ("era") effect as a covariate of ψ within a single-season model. To account for heterogeneity in detection frequencies, we tested between six different 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. Continuous covariates were standardized to have a mean 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 full detection model is described as:

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

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

Building on the model used by Moritz et al. (2008), single-season occupancy parameterizations sought to examine how occupancy changed over time (*era*), over elevation (*elevation* and $elevation^2$), and among the three regions (defined by two dummy variables, *R1* and *R2*). We tested 25 different ψ parameterizations, which included all combinations of these covariates along with all 2- and 3-way interaction terms and a null (intercept-only) model (full model set listed in Table S1). Our final model set combined all p parameterizations with all ψ parameterizations, resulting in 150 competing models that were run on each species and compared using AIC_c (Burnham and Anderson 2002). Unconditional, model-averaged values of $p_{i,j,k}$ and $\psi_{i,j}$ were calculated using AIC_c weights (w_i) of each model (Burnham and Anderson 2002). All occupancy models were run in R version 2.12 (R Development Core Team 2010) based on code modified from Royle and Dorazio (2008).

Estimation of elevational ranges and estimation of change

We estimated elevational range change at the inferred limits and centers of distributions. To quantify changes to range limits, we used a P_{fa} (probability of false absence) test on both lower and upper elevational 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 at a set of sites at the lower or upper range boundary but was not detected (Moritz et al. 2008, Tingley and Beissinger 2009). Range limit shifts with a $P_{fa} \leq 0.05$ were statistically significant.

Variations at range margins can mask underlying shifts in centers of distributions, including leaning or skewed distributions (Breshears et al. 2008, Kelly and Goulden 2008). Past studies have measured distribution shifts by using the maximum probability of occurrence to determine the center (Wilson et al. 2005, Lenoir et al. 2008). However, this method does not work when elevational distributions are not quadratic in shape (Tingley and Beissinger 2009). Consequently we calculated the distributional center, or median, as the elevation at which exactly half of the cumulative occupancy curve lies above and below. We defined this "range center" as conditional upon:

$$\int_{\min(\mathbf{x})}^{M} \Pr(\psi) = \int_{M}^{\max(\mathbf{x})} \Pr(\psi)$$

where **x** is the set of elevations at which surveys were conducted. The range center represents a single value that, as desired, does not change if both upper and lower elevational bounds equally contract (or expand; Figure S3).

For all range metrics – limits and centers – we further added a condition of "ecological significance" (Moritz et al. 2008) by which range shifts were measured. A range shift was considered ecologically significant if the magnitude of the shift was greater than 5% of the species' historic elevational range within a specific region. While Moritz *et al.* used a criterion of 10%, their study only examined shifts at range boundaries, not range centers. Range limits are far more variable than range centers (Brown et al. 1996), and thus a more sensitive cut-off was selected.

Climate and nearest neighbor predictions

Trends in average annual climate (Figure 2a-c) were ascertained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM). PRISM uses mathematical interpolation of historical weather data along with expert knowledge of bioclimatic processes to provide monthly climate surfaces dating back to 1890 (Daly et al. 2002). We used surfaces with 1 x 1 km spatial resolution (received 1/26/2009, C. Daly pers. comm.) to quantify both historical (1910-1930) and modern (1989-2009) average annual temperature and precipitation at each of our survey locations (Figure 2a-c).

Nearest neighbor elevations were built on methods developed by 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 (Figure S1). The regional set comprised all 1 x 1 km PRISM grid cells within a geographic area defined by a minimum convex polygon plus 10 mile buffer surrounding all survey localities in a region. The cell with the minimum modern climatic distance from a survey site's historic climate was assigned as the nearest modern climatic neighbor (Figure S1b-c). Sites were only compared to climates of cells within the same region. Comparing the elevations of each site and its nearest modern climatic neighbor allowed the creation site-specific predictions of elevational change for each survey site (Figure 2d-f) and for every grid cell within each region (Figure S2). Upper and lower limit predictions for each species were determined by the nearest neighbor elevation for the actual sites where the species had its historical upper and lower limit. Range center predictions were derived from the site closest to the measured historical range center.

Analyses of correlates of range change

Individual species' patterns of range change (upper bound, lower bound, and center) were analyzed using Generalized Linear Mixed Models (GLMM) to examine whether species' traits could explain whether species moved or not, and whether regional and life zone differences explained whether species shifted range up or down. Life history data was compiled for all species based on accounts from *The Birds of North America Online* (Poole 2005). We determined: (1) whether the species is a year-round resident of California (including short-distance migrants) or a neotropical migrant; (2) average mass of breeding adult (average of male and female masses of California subspecies, when available); (3) whether the species defends all-purpose "Type-A" (Nice 1941) territory versus any other territory type; (4) average home range size (ha) of breeding individuals; (5) average clutch size of females (data from California, when available); and (6) whether the species was a dietary generalist (e.g., omnivore) or had a restricted diet. Data on all trait measures were available for 86 of the 99 focal species (Table S2).

GLMMs were used to analyze whether the probability of an elevational shift in each of the three range change metrics was related to: (1) the elevational zone of the species, as determined by the historical classification into different life-zones in Grinnell's monographs (Grinnell and Storer 1924, Grinnell et al. 1930); (2) the region of the Sierra Nevada; and (3) species traits. To assign elevational zone we followed Moritz et al. (2008). Species that reached their highest historical classification in the Transition life-zone or below were identified as "low elevation species," while species that reached their highest historical classification in the Canadian, Hudsonian, or Alpine life-zones were labeled as "high elevation species." These factors were tested as predictors of range change in a two-part process using a binomial GLMM with species identity as a random factor. First, elevational zone and region were tested separately and in the same model with interactions, and the best fitting model (as measured by AIC) was selected. Second, each species trait was added as a factor to the best fitting model from the previous step to see if life history information improved model fit, as measured by AIC. Multiple traits were added to models *ad hoc* until additional traits no longer improved AIC score. GLMM models were run in R version 2.12 (R Development Core Team 2010) using the package 'lme4' (Bates and Maechler 2010) according to recommendations in Zuur et al. (2009).

Results

Sierra Nevada bird species, on the whole, have shifted upward in elevational range over the last century (Figure 3). Across all 99 focal species, 85% shifted their elevational range upward in at least one region, and 68% of species significantly shifted up for at least one range metric (Table S3). Upward shifts varied in magnitude with a range of 70 – 1155 m for lower limits, 25 – 1217 m for range centers, and 137 – 2503 m for upper limits. Across all three metrics, 12% of upward range shifts, derived from 16 species, were greater than 1 km.

Range shifts were heterogenous across regions. Of the 53 species analyzed in all three regions, only seven species (13%) significantly shifted upward in elevational range throughout the Sierra Nevada for at least one metric (Fox Sparrow, Lazuli Bunting, Spotted Towhee, Red-breasted Sapsucker, Chipping Sparrow, Mountain Bluebird, and Mourning Dove). In contrast, two species showed downward movements of one metric across all three regions (Ash-throated Flycatcher and Wilson's Warbler). Of the remaining 44 species, approximately 71% shifted up in one or two regions for at least one metric.

Patterns of upward range shift, as supported by model-averaged GLMMs, showed a high degree of variability among range metrics and by species' elevational zone (Figure 4). Range centers were the only metric to show consistent upward movements, with high-elevation species significantly more likely to shift up than down in the northern and central regions (Figure 4). Elevational zone had a strong effect on the likelihood of a species shifting its range limits. High elevation species were more likely to shift lower limits up, while low elevation species were more likely to shift upper limits up (Figure 4). These patterns differed in strength by region, with the central Sierra Nevada having the greatest probability of a species expanding its upper limit, and the northern Sierra Nevada having the greatest probability of a species contracting its lower limit.

A naïve hypothesis expecting all species in all regions to have shifted upslope describes no more than 56% of the results observed (Table 1). Instead, site-specific expectations of range shift incorporating nearest climatic neighbors greatly increased the proportion of species that met expectations (Figure 5, Table 1). For all three range metrics, the fraction of species observed shifting up approximately matched the fraction of species with movements agreeing with temperature-based nearest neighbors predictions (Figure 5). The northern region was an exception; minor, localized cooling there predicted downward shifts (Figure 2a,d), particularly for the upper limit of high elevation species, that were unexplained by the naïve expectation of upward movement (Figure 5a). Overall, temperature explained a marginally greater percentage of observed movements than precipitation (Table 1). In the southern region, however, precipitation explained a greater proportion of upper and lower limit movements. Lower limit shifts were better explained by precipitation than temperature for all regions.

Since it is unknown *a priori* whether a species in a particular region is more likely to shift in response to temperature or precipitation, we tested whether either factor could explain the observed movement (Figure 5, Table 1). Across all regions, the upward or downward directions of 88% of upper limit shifts, 81% of range center shifts, and 75% of lower limit shifts agreed with expectations derived from either temperature or precipitation (Table 1). In total, 82% of all measured range shifts moved in the same direction as predicted by the difference in elevation between a historic survey site and its modern climatic nearest-neighbor as measured by either temperature or precipitation.

Although climate strongly predicted directions of range shifts, over a quarter of the species in each region did not shift elevational range, despite regional climatic expectations to do so. However, some species traits were related strongly to whether a species shifted range or not, improving models for all three range metrics (Table 2). These species trait relationships held after controlling for phylogeny by adding family as a random factor. Species with small clutch sizes were significantly (Wald test: $P = 0.001$) more likely to shift range than species with large clutch sizes (Figure 6a). Additionally, species with type-A territories had 3.3 times greater odds of shifting ranges than less territorial (i.e., non A-type) species (95% CI odds ratio: 1.5 – 7.6). Range centers (Figure 6b) had a similar relationship, with species with type-A territories having 15.3 times greater odds of shifting than species with other territory types (95% CI odds ratio: 1.9 – 122.7). Finally, there were significant differences in the probability of lower limit range shifts by region and by migratory status (Wald test: $P = 0.005$). Species that reside in California year-round had 5.3 times greater odds of shifting lower range limits than species that migrate to Central or South America (95% CI odds ratio: 1.6 – 17.5, Figure 6c).

Discussion

We have presented 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 image emerges of how climate change has drastically altered the distributions of the biotic community. Our results highlight, however, that distribution change is not unidirectional; rather, there is a high degree of variation, with differences 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 average warming temperatures, our results caution that climate change impacts on species' ranges, including likely future shifts, are highly variable, with species- and region-specific differences.

Meeting predictions: temperature versus precipitation

Our results demonstrate that site-specific expectations of the direction of elevational shift, based on the climate history of a site, were substantially more successful at predicting observed shifts than the naïve hypothesis that all species will shift up. Only 57%, 63% and 50% of species' range metrics shifted upslope for the northern, central and southern regions, respectively. However, 78%, 81% and 88%, respectively, of changes to range boundaries or range centers shifted upslope or downslope in accordance with nearest climatic neighbor expectations (Table 1). Additionally, the northern Sierra Nevada has barely warmed on average over the last century, showing localized areas of marginal warming and cooling (Figure 2), yet the region showed a percentage of species shifting comparable to the other two regions (Figure 3). Thus, as a control region for average warming, the northern Sierra Nevada illustrates the failure of the naïve hypothesis to predict range shifts.

The biggest improvement to predictions came from incorporating precipitation changes into expectations. While temperature decreases with altitude, leading to expectations of upslope shifts as climate warms, precipitation patterns can provide opposite expectations. Generally, precipitation increases with elevation, and the climate trend over the last century has resulted in increased precipitation (Figure 2a-c). Consequently, for many parts of the Sierra Nevada, species sensitive to precipitation may be expected to shift downslope (Figure 2d-f). Precipitation by itself explained 63%, 50% and 64% of shifts for the northern, central, and southern regions, respectively. Yet, precipitation and temperature together were able to explain all but 10-20% of range shifts (upslope and downslope). This is consistent with the result of Tingley et al. (2009) who found that patterns of occurrence change in Sierra Nevadan birds showed species differentially tracking a climatic niche defined by either temperature or precipitations. Similarly, Crimmins et al. (2011) found that precipitation played a critical role in explaining the 72% of plant species that shifted downslope in California since the 1930s. It is possible that precipitation could also explain the 28% of downslope range shifts observed in mammals in the Yosemite region of California (calculated from Figure 3a in Moritz et al. 2008). While the opposing pull of temperature and precipitation may best describe the majority of 20th century elevational shifts for species, how temperature and precipitation are likely to influence species' ranges in the future is more uncertain. Whether we expect future conditions to be warmer and wetter or warmer and drier, for instance, can significantly change the direction in which species are expected to move (Ackerly et al. 2010).

Variability in response to climate

Precipitation and temperature are likely to have differing strengths of influence on different species and in different regions. Generally, low elevation species' ranges are limited by biotic factors (i.e., species interactions), while high elevation species' ranges are limited by abiotic factors (Brown et al. 1996). However, Tingley et al. (2009) found that low elevation birds in the Sierra Nevada were more likely to have shifted their occurrence in climate space toward more favorable precipitation conditions, while high elevation species shifted toward more favorable temperature conditions. Consistent with this pattern, we found that lower limits had movement patterns best described by precipitation, while upper limits (in the northern and central regions) had movement patterns best described by temperature (Table 1).

Our results also highlight the importance of local climatic conditions in creating variability in measured elevational shifts. Of the 53 species with range shifts tested for all three regions, 34% shifted elevational centers in opposite directions across different Sierra Nevada regions (51% for upper range boundary, 42% for lower range boundary). This variation could be explained by species responding to different climate change in each region. For instance, in the southern region, which is the warmest and the driest (Figure 2a), precipitation explained a greater proportion of range limit movements (Table 1). Grinnell (1917b) posited that different factors limited distributions across a species' geographic range. Modern theory concurs, positing that different biotic or abiotic factors can switch from non-limiting 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 provide strong empirical support for these theoretical expectations.

The three metrics of range change that we used provided contrasting measures of how species are shifting. Elevational range change studies often only use one metric to represent either the center of the range (e.g., Archaux 2004, Lenoir et al. 2008, Crimmins et al. 2011) or its limits (e.g., Peh 2007, Moritz et al. 2008). Yet, comparing both types of measures can describe different processes by which populations expand or contract their range (Breshears et al. 2008, Maggini et al. 2011). For instance, a range center may shift up while the range limits remain stable if the upper boundary is prevented from shifting by a barrier, such as habitat (Maggini et al. 2011). In our study, climate-based hypotheses of range shift were more successful at explaining upper boundary shifts than lower boundary shifts, and to a lesser extent, at explaining high elevation species' shifts than low elevation species' shifts. Lower limits have strong theoretical support for being sensitive to species interactions such as competition or predation (Lenoir et al. 2010), and the disruption of these interactions could be driving lower limit shifts. Moreover, low elevation species and lower limits are far more likely to have been affected by land-use change in our study regions; although we resurveyed in the same habitats and general locations as historical samples, exurban in-fill and agricultural and grazing intensification were unavoidable at low elevations. Also, these findings may partly result from low sample sizes; species shifted their lower limits approximately 40% less often than they shifted their upper limits. A certain portion of range shifts, particularly range limits that are susceptible to vagrants and pioneering individuals (Grinnell 1922), are expected to occur as "random" fluctuations (Lenoir et al. 2010). With fewer species in the shifting pool, each species that shifts as a result of local demographic or stochastic processes exerts a greater bias on observing the overall trend.

To shift or not to shift

Of critical importance to conservation are reasons why species do not shift their ranges given climate change. Of the species that did not shift their range centers in at least one region, 68% did not shift in any region (60% for lower limits, 48% for upper limits). Ten out of 53 species analyzed across all three regions did not shift by any metric in any region. The theoretical reasons why species may not shift given climatic change are many. Adaptation through micro-evolution is theoretically possible (Rodríguez-Trelles and Rodríguez 1998), yet it is unlikely that vertebrates can adapt as quickly as necessary (Gienapp et al. 2008, Visser 2008, Sinervo et al. 2010). Species may also be limited by dispersal (Davis et al. 1998b, Svenning et al. 2008), leading to a failure to shift or a lag in response observed as a failure (La Sorte and Jetz in review). Additionally, species may hold a constant distribution if the climate of the occupied range is shifting towards the center of the species' niche, but not toward the niche boundary (Tingley et al. 2009).

We found that some species traits had strong relationships with range shifts (Figure 6), even when partially controlling for phylogeny (Angert et al. in review). Surprisingly, these relationships were opposite to the dispersal-related hypotheses generated *a priori*: species were more likely to change range if they had smaller clutches, held defined territories for feeding and breeding, and were year-round residents of California (i.e., short-distant or migratory species). Thus, an alternative hypothetical framework could relate the likelihood of a range shift with behavioral plasticity over the life span of an individual. For instance, neotropical migrants are known to have shorter life spans than resident species (Martin 1995), and clutch size is typically inversely related with longevity (Sæther 1988, Martin 1995). Climate change is expected to impact bird ranges through the indirect pathways of changing food availability and nest success

(Sanz et al. 2003, Both et al. 2006), both of which are known to directly impact breeding site fidelity (Greenwood and Harvey 1982, Hoover 2003). It is unproven whether there is a relationship between nest-site fidelity and longevity, yet by definition long-lived birds have more opportunities to incorporate breeding success knowledge 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, Both et al. 2011), species holding feeding territories might have greater pressures to define climatically favorable (and thus food-resource favorable) territories than species that travel great distances in search of food. Our species' trait analysis suggests that it is not the physical ability to disperse that is preventing bird species from shifting their range. Rather, the evidence points to a complex interplay between the differential effects of climate change and phenological shifts on nest-site selection among birds of different life history patterns. The strength of this relationship deserves to be tested with empirical data.

Table 1. Summary of the percentage of range shifts meeting four hypotheses of how species are expected to shift ranges. Numbers in each cell are the percentage of species followed by the sample size of species in parentheses.

Range Metric	Hypothesis	Northern	Central	Southern	All Regions
Upper	naïve	43 (40)	69 (35)	50 (34)	53 (109)
	temperature-only	75 (40)	66 (35)	41 (34)	61 (109)
	precipitation-only	65 (40)	46 (35)	56 (34)	56 (109)
	t & p combined	80 (40)	91 (35)	94 (34)	88 (109)
Median	naïve	68 (34)	77 (30)	55 (31)	66 (95)
	temperature-only	44 (34)	77 (30)	45 (31)	55 (95)
	precipitation-only	50 (34)	50 (30)	39 (31)	46 (95)
	t & p combined	74 (34)	93 (30)	77 (31)	81 (95)
Lower	naïve	69 (16)	38 (26)	44 (25)	48 (67)
	temperature-only	50 (16)	35 (26)	60 (25)	48 (67)
	precipitation-only	63 (16)	50 (26)	64 (25)	58 (67)
	t & p combined	81 (16)	54 (26)	92 (25)	75 (67)
Combined	naïve	57 (90)	63 (91)	50 (90)	56 (271)
	temperature-only	59 (90)	60 (91)	48 (90)	56 (271)
	precipitation-only	59 (90)	48 (91)	52 (90)	53 (271)
	t & p combined	78 (90)	81 (91)	88 (90)	82 (271)

Table 2. AIC results of GLMM analyses for tests of factors that relate to whether species shifted versus did not shift their upper range boundary, range center, or lower range boundary. For each range metric, "basic" models were first tested to control for broad differences among species. The best-ranked "basic" model was then used as a base model to individually test species traits. Models that included multiple species traits were not tested unless more than one trait improved AIC score above the base model. Species identity and species family were treated as random effects in models to control for pseudoreplication and phylogeny. For explanations of life history covariates, see Methods.

Range metric	Model[*]	Parameter	K	AIC	ΔAIC	AIC Wt (*w*)
Upper limit	Basic	Zone[†]	3	260.4	0.0	0.68
		Region + Zone	5	262.6	2.2	0.23
		Region x Zone	7	264.9	4.5	0.07
		Null[‡]	2	267.2	6.8	0.02
		Region	4	270.3	9.9	0.00
	Traits	Clutch size + Territoriality + Zone	7	244.3	0.0	0.46
		Clutch size + Territoriality + California year-round resident + Zone	8	244.4	0.1	0.44
		Clutch size + CA Resident + Zone	7	249.3	5.0	0.04
		Territoriality + CA Resident + Zone	7	250.2	5.9	0.02
		Clutch size + Zone	6	250.4	6.1	0.02
		Territoriality + Zone	6	252.9	8.6	0.01
		CA Resident + Zone	6	255.6	11.3	0.00
		Zone (base model)	5	260.4	16.1	0.00
		Mass + Zone	6	260.6	16.3	0.00
		Omnivore + Zone	6	261.7	17.4	0.00
		Home range + Zone	6	262.2	17.9	0.00
Range center	Basic	Null	2	226.3	0.0	0.57
		Zone	3	227.6	1.3	0.30
		Region	4	230.3	4.0	0.08
		Region + Zone	5	231.5	5.2	0.04
		Region x Zone	7	235.3	9.0	0.01
	Traits	Territoriality	3	223.9	0.0	0.33
		Territoriality + Clutch size	4	224.2	0.3	0.28
		Clutch size	3	225.7	1.8	0.13
		Null (base model)	2	226.3	2.4	0.10
		Home range	3	227.7	3.8	0.05
		Omnivore	3	228.2	4.3	0.04
		CA resident	3	228.3	4.4	0.04
		Mass	3	228.3	4.4	0.04
Lower limit	Basic	Region + Zone	5	227.3	0.0	0.41
		Region	4	227.5	0.2	0.38
		Null	2	229.9	2.6	0.11
		Zone	3	230.2	2.9	0.10
		Region x Zone	7	NA	-	-
	Traits	CA resident + Region + Zone	6	223	0.0	0.71
		Region + Zone (base model)	5	227.3	4.3	0.08
		Territoriality + Region + Zone	6	228.5	5.5	0.05
		Omnivore + Region + Zone	6	228.5	5.5	0.05

	Clutch size + Region + Zone	6	228.5	5.5	0.05
	Home range + Region + Zone	6	228.6	5.6	0.04
	Mass + Region + Zone	6	229.3	6.3	0.03

[*] Basic models are GLMMs testing only simple hypotheses of variation in movement patterns such as survey region or elevational zone. Life history models take both the best fitting (lowest AIC) basic model and the null model, and individually test the added explanatory power of including individual life history traits.

[†] Zone is a binary variable indicating whether species are *a priori* classified as “low elevation” or “high elevation.”

[‡] The null model is a model with no fixed effects, only an intercept and the random effect of species.

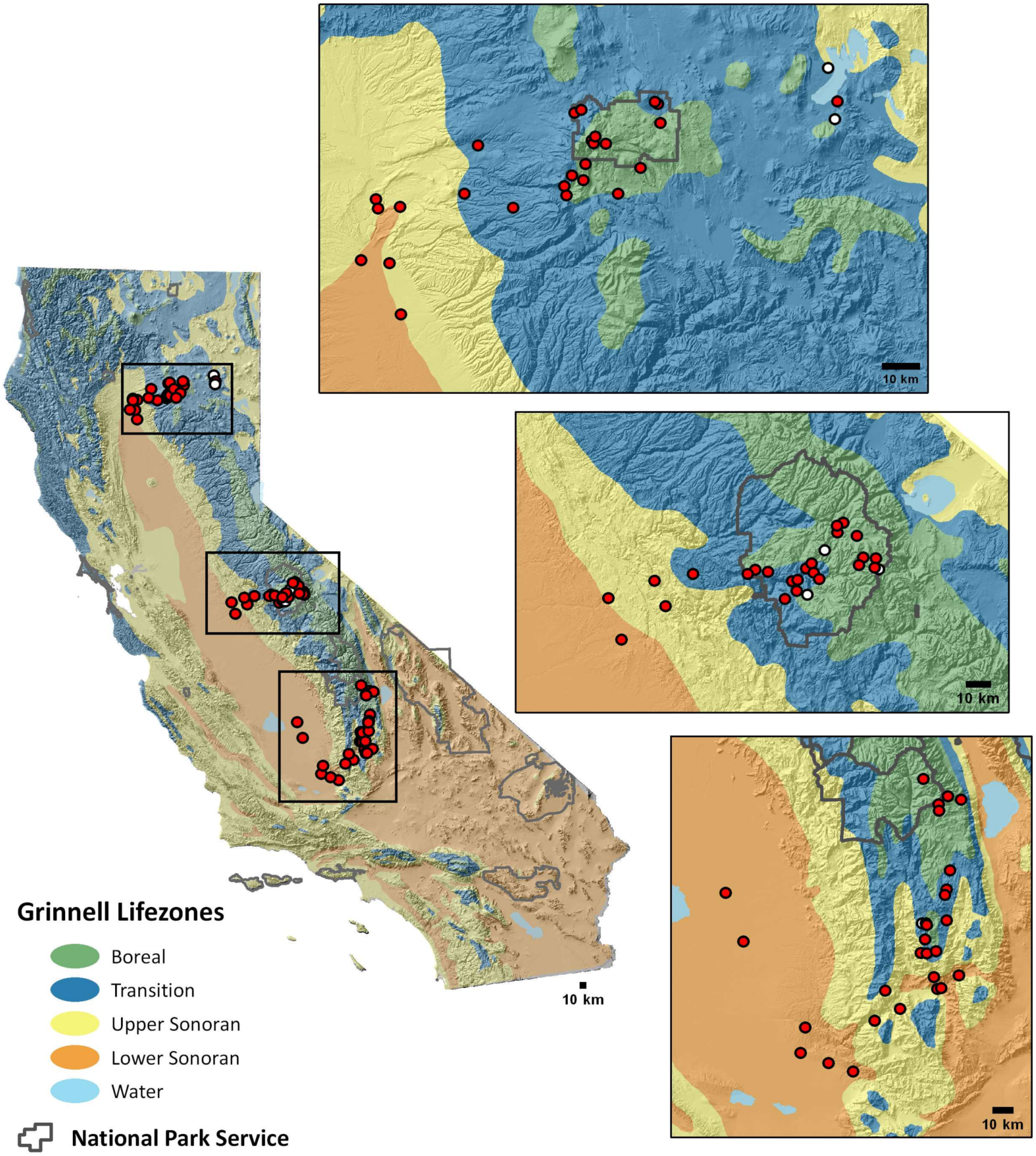


Figure 1. Locations in California of three elevational cross-sections of the Sierra Nevada showing locations of resurvey sites superimposed on top of topography and Grinnell's life zones (Grinnell & Storer, 1924). A total of 77 historical sites were revisited (red), with new surveys conducted at seven sites (white). US National Parks are outlined in gray.

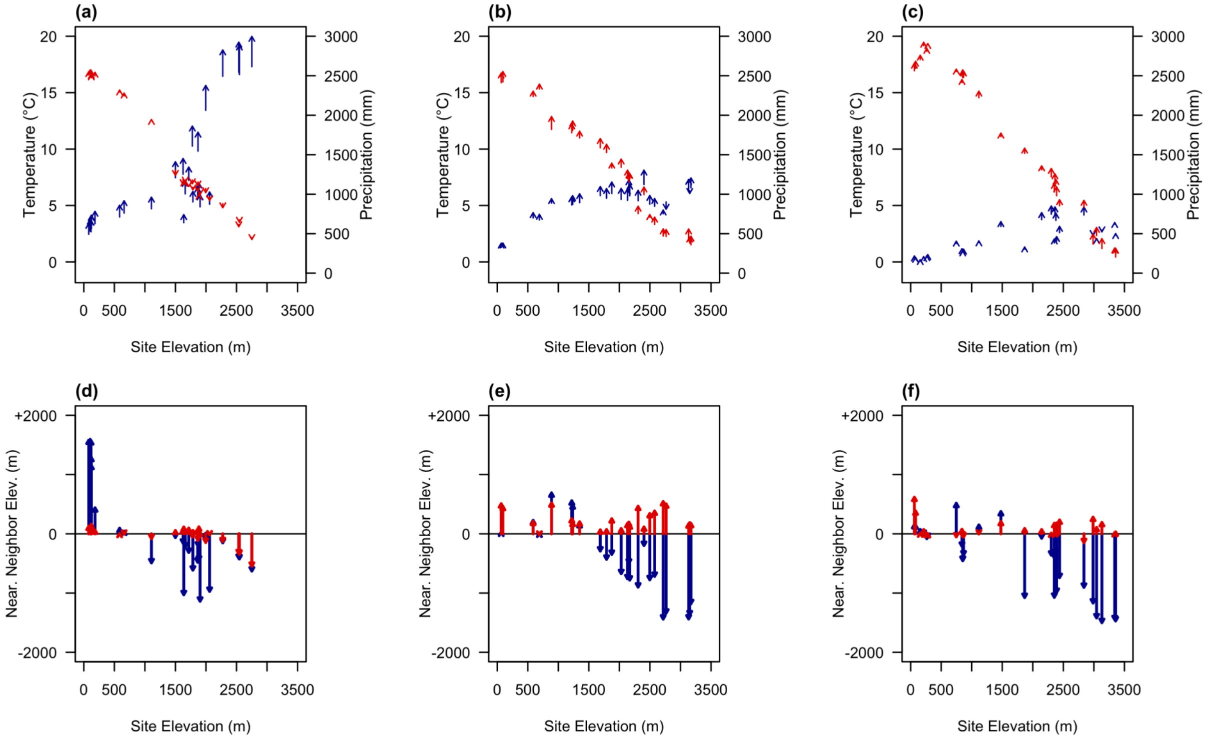


Figure 2. Climate history (a-c) and nearest climate neighbor elevations (e-g) for resurvey sites in the northern (a,d), central (b,e) and southern (c,f) Sierra Nevada survey regions. Changes in average annual temperature (red arrows) and precipitation (blue arrows) between 1900-1930 and 1980-2006 are shown for survey sites in each region (a-c). Arrows point from the average historical climate at a site to the average modern climate at a site. Comparing among regions highlights differences in minimum, maximum, and rate of change of climate with elevation between sections of the Sierra Nevada. Sites with a particular historic average temperature or precipitation are unlikely to be their own modern temperature or precipitation nearest neighbor given climate change. The difference in elevation between each site and the elevation of the site's nearest climatic nearest neighbor are illustrated for temperature (red arrows) and precipitation (blue arrows) for each region (d-f). Positive differences in nearest neighbor elevation (arrows above the black line) indicate that a species at a particular point would need to shift up in elevation to stay as close as possible to historic climatic average conditions at that point.

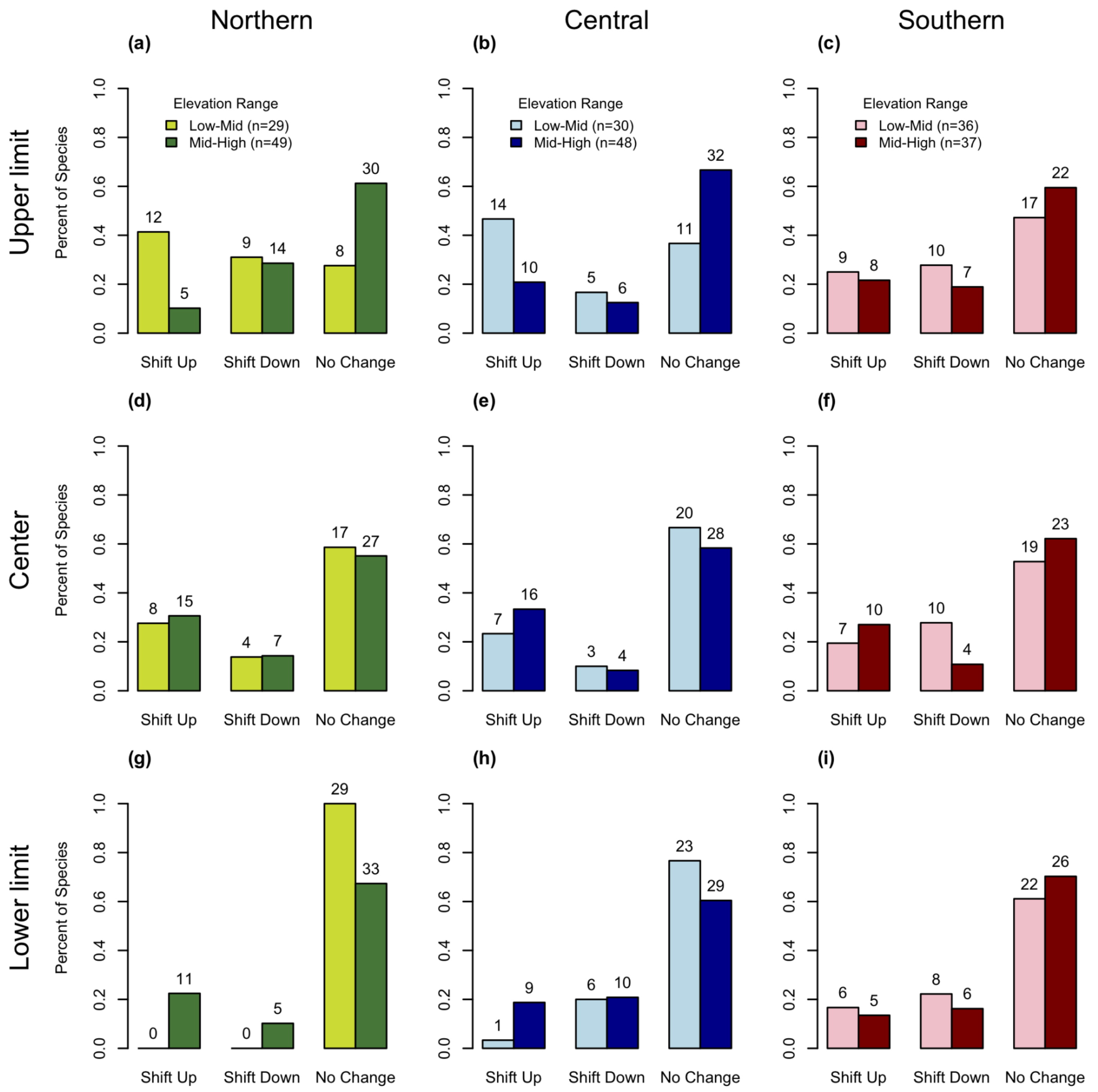
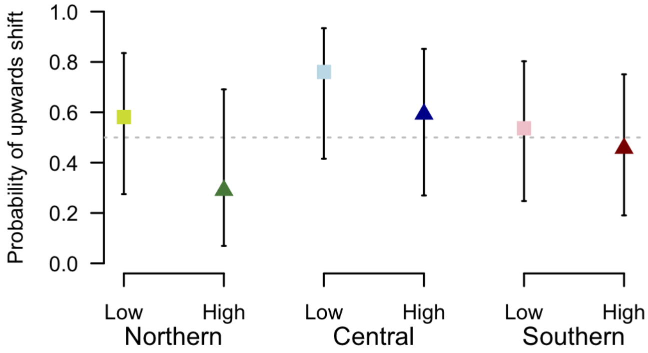
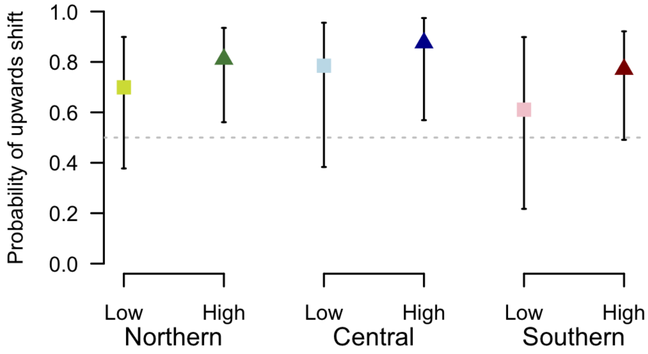


Figure 3. Elevational change in species range for range change metrics (rows), regions of Sierra Nevada (columns), and elevational zones (bar colors within each graph). Numbers of species in each category are listed above bars. Only species with range shifts greater than 5% of their historical elevational range are categorized as having moved.

(a) Upper limit



(b) Range center



(c) Lower limit

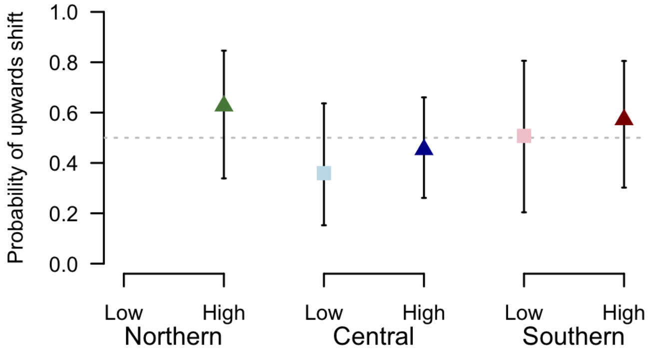
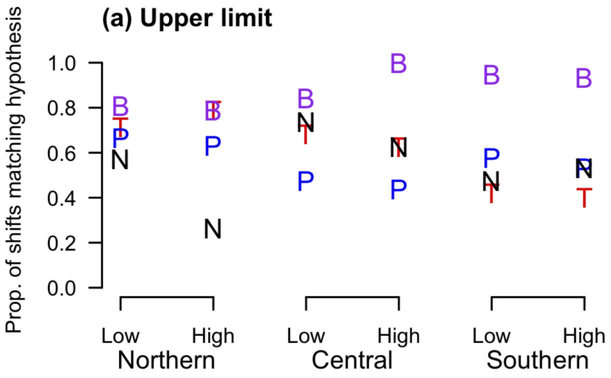
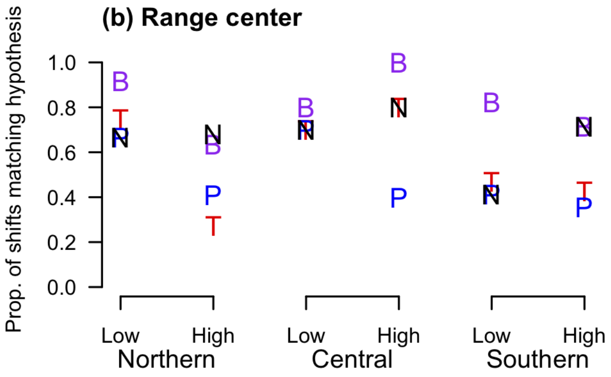


Figure 4. The mean and 95% confidence interval of the probability of a species shifting up versus down in elevation, for upper limits (a), range centers (b), and lower limits (c) in each region (northern = green, central = blue, southern = red) and species' elevational zone (squares = low elevation species, triangles = high elevation species). Point estimates are model-averaged outcomes of six competing GLMM logistic models. No low-elevation species in the Northern region shifted its lower range limits in any direction.

(a) Upper limit



(b) Range center



(c) Lower limit

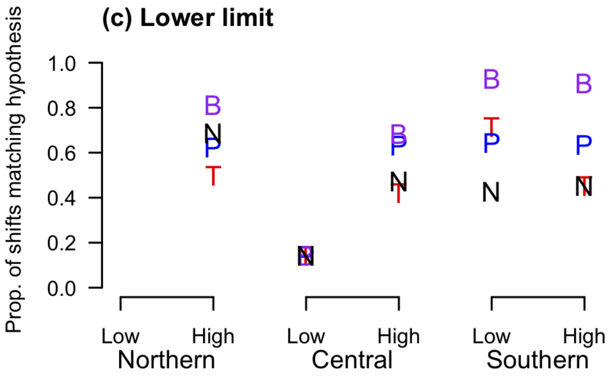


Figure 5. The proportion of species with upper limit (a), range center (b), and lower limit (c) shifts whose directions (shift up or shift down) concur with various predictive hypotheses. The naïve hypothesis (black "N") specified that, consistent with average warming, all species should shift up. The remaining hypotheses were derived from site-specific predictions based on the change in elevation from historic to modern of a site's nearest temperature (red "T") or precipitation (blue "P") neighbor. Since it is unknown whether a species at a particular site is more likely to respond to temperature or precipitation, a combined predictive hypothesis (purple "B") tested whether either temperature or precipitation explained the direction of the shift. Species that did not shift in the relevant metric were considered non-informative and were excluded from counts for this figure.

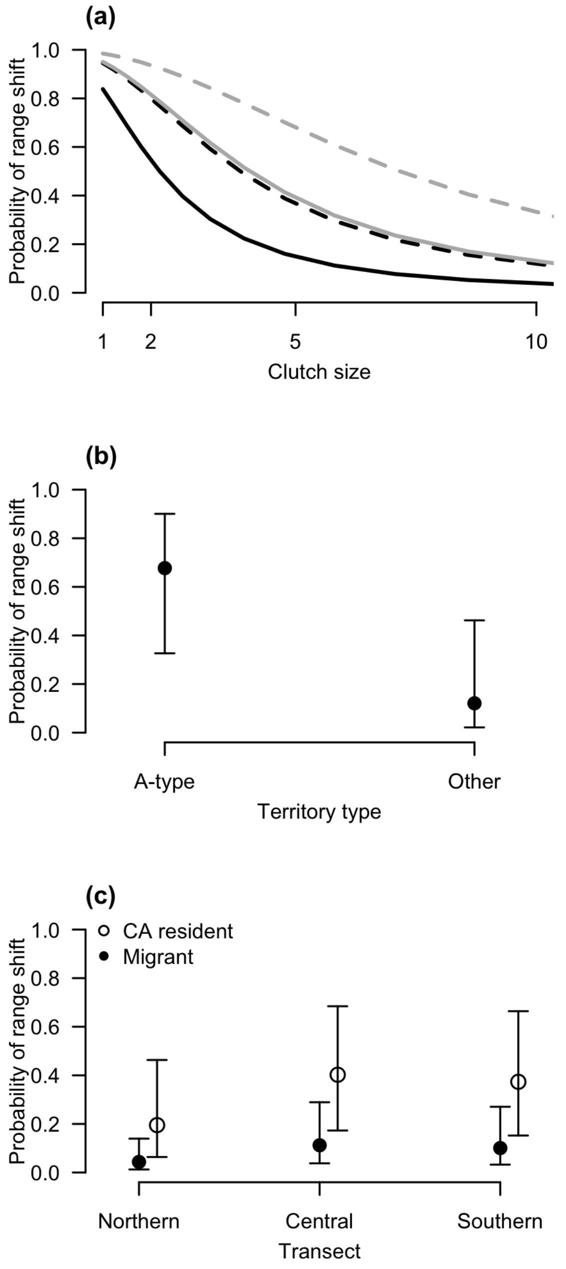


Figure 6. Significant explanatory relationships between species' traits and the probability of a shift (up or down) of different range metrics. Upper limits (a) were significantly more likely to shift for low clutch-sized species, in addition to being more likely to shift for low-elevation species (gray lines) than high-elevation species (black lines), and strongly-territorial (A-type) species (dotted lines) than less-territorial species (solid lines). Range centers (b) were also more likely to shift for A-type territorial species, while lower limits (c) differed slightly by region and were significantly more likely to shift for year-round resident species of California (open circles) than neotropical migrants (solid circles).

Table S1. Descriptions and parameterizations of 25 occupancy (ψ) models with main, additive and multiplicative effects. Parameterization shows fitted coefficients (β_i) and site-specific covariates (*era*, the time period in which the survey was conducted; *elev* and *elev*^{2}, the scaled and scaled-quadratic site elevation; and $R1$ and $R2$, which are region-specific indicator variables).

No.	Description	Parameterization
1	Null	$\text{logit}(\psi) = \beta_0$
2	Era	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era$
3	Elev	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev$
4	Elev^2	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev + \beta_2 \cdot elev^2$
5	Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot R1 + \beta_2 \cdot R2$
6	Era + Elev	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev$
7	Era + Elev^2	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2$
8	Era x Elev	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot era \cdot elev$
9	Era x Elev^2	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot era \cdot elev + \beta_5 \cdot era \cdot elev^2$
10	Era + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot R1 + \beta_3 \cdot R2$
11	Era x Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot R1 + \beta_3 \cdot R2 + \beta_4 \cdot era \cdot R1 + \beta_5 \cdot era \cdot R2$
12	Elev + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev + \beta_2 \cdot R1 + \beta_3 \cdot R2$
13	Elev^2 + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev + \beta_2 \cdot elev^2 + \beta_3 \cdot R1 + \beta_4 \cdot R2$
14	Elev x Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev + \beta_2 \cdot R1 + \beta_3 \cdot R2 + \beta_4 \cdot elev \cdot R1 + \beta_5 \cdot elev \cdot R2$
15	Elev^2 x Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot elev + \beta_2 \cdot elev^2 + \beta_3 \cdot R1 + \beta_4 \cdot R2$ $+\beta_5 \cdot elev \cdot R1 + \beta_6 \cdot elev \cdot R2 + \beta_7 \cdot elev^2 \cdot R1 + \beta_8 \cdot elev^2 \cdot R2$
16	Era + Elev + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot R1 + \beta_4 \cdot R2$
17	Era + Elev^2 + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot R1 + \beta_5 \cdot R2$
18	Era x Elev + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot era \cdot elev + \beta_4 \cdot R1 + \beta_5 \cdot R2$
19	Era x Elev^2 + Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot era \cdot elev + \beta_5 \cdot era \cdot elev^2$ $+\beta_6 \cdot R1 + \beta_7 \cdot R2$
20	Era + Elev x Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot R1 + \beta_4 \cdot R2$ $+\beta_5 \cdot elev \cdot R1 + \beta_6 \cdot elev \cdot R2$
21	Era + Elev^2 x Region	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot R1 + \beta_5 \cdot R2$ $+\beta_6 \cdot elev \cdot R1 + \beta_7 \cdot elev \cdot R2 + \beta_8 \cdot elev^2 \cdot R1 + \beta_9 \cdot elev^2 \cdot R2$
22	Era x Region + Elev	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot R1 + \beta_4 \cdot R2$ $+\beta_5 \cdot era \cdot R1 + \beta_6 \cdot era \cdot R2$

23	Era x Region + Elev^2	$\operatorname{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot R1 + \beta_5 \cdot R2$ $+\beta_6 \cdot era \cdot R1 + \beta_7 \cdot era \cdot R2$
24	Era x Elev x Region	$\operatorname{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot R1 + \beta_4 \cdot R2 + \beta_5 \cdot era \cdot R1$ $+\beta_6 \cdot era \cdot R2 + \beta_7 \cdot elev \cdot R1 + \beta_8 \cdot elev \cdot R2 + \beta_9 \cdot era \cdot elev$ $+\beta_{10} \cdot era \cdot elev \cdot R1 + \beta_{11} \cdot era \cdot elev \cdot R2$
25	Era x Elev^2 x Region	$\operatorname{logit}(\psi) = \beta_0 + \beta_1 \cdot era + \beta_2 \cdot elev + \beta_3 \cdot elev^2 + \beta_4 \cdot R1 + \beta_5 \cdot R2$ $+\beta_6 \cdot era \cdot R1 + \beta_7 \cdot era \cdot R2 + \beta_8 \cdot elev \cdot R1 + \beta_9 \cdot elev \cdot R2 + \beta_{10} \cdot era \cdot elev$ $+\beta_{11} \cdot elev^2 \cdot R1 + \beta_{12} \cdot elev^2 \cdot R2 + \beta_{13} \cdot era \cdot elev^2$ $+\beta_{14} \cdot era \cdot elev \cdot R1 + \beta_{15} \cdot era \cdot elev \cdot R2$ $+\beta_{16} \cdot era \cdot elev^2 \cdot R1 + \beta_{17} \cdot era \cdot elev^2 \cdot R2$

Table S2. Life history and other species characteristics used in traits analysis. Species are listed in taxonomic order. For descriptions of traits, see Methods.

English Name	Family	Primary life zone	Elevational zone	California year-round resident	Average mass (g)	Territoriality	Average home range (ha)	Average clutch size	Omnivorous
Mountain Quail	Odontophoridae	Canadian	High	-	-	-	-	-	-
California Quail	Odontophoridae	Upper Sonoran	Low	yes	175	other	7.5	11	no
Dusky Grouse	Phasianidae	Canadian	High	-	-	-	-	-	-
Band-tailed Pigeon	Columbidae	Transition	Low	yes	391	other	11121	1	no
Mourning Dove	Columbidae	Upper Sonoran	Low	yes	112	other	1600	2	no
Black-chinned Hummingbird	Trochilidae	Upper Sonoran	Low	no	3.3	A-type	320	2	yes
Anna's Hummingbird	Trochilidae	Upper Sonoran	Low	yes	4.3	A-type	1.2	2	yes
Calliope Hummingbird	Trochilidae	Canadian	High	-	-	-	-	-	-
Acorn Woodpecker	Picidae	Upper Sonoran	Low	yes	79.1	other	6	5.06	yes
Williamson's Sapsucker	Picidae	Hudsonian	High	yes	47.6	A-type	6.75	4.4	yes
Red-breasted Sapsucker	Picidae	Transition	High	yes	58	A-type	5.9	4.69	yes
Nuttall's Woodpecker	Picidae	Upper Sonoran	Low	yes	38.3	A-type	65	4.57	yes
Downy Woodpecker	Picidae	Transition	Low	yes	27.9	A-type	5.5	4.81	yes
Hairy Woodpecker	Picidae	Canadian	High	yes	65.5	A-type	2.6	3.93	yes
White-headed Woodpecker	Picidae	Transition	High	yes	61.1	A-type	200	4.28	no
Northern Flicker	Picidae	Upper Sonoran	High	yes	157	other	25	6.5	no
Pileated Woodpecker	Picidae	Transition	High	yes	288	A-type	407	3.82	no
Olive-sided Flycatcher	Tyrannidae	Canadian	High	no	33.2	A-type	45	3.02	no
Western Wood-Pewee	Tyrannidae	Transition	High	no	12.9	A-type	1.7	3	no
Willow Flycatcher	Tyrannidae	Transition	High	no	12.6	A-type	1.72	3.7	no
Hammond's Flycatcher	Tyrannidae	Canadian	High	no	10.5	A-type	1.05	4	no
Dusky Flycatcher	Tyrannidae	Canadian	High	no	10.4	A-type	0.73	4	no
Pacific-slope Flycatcher	Tyrannidae	Transition	Low	no	10.7	A-type	2.5	3.3	no
Black Phoebe	Tyrannidae	Lower Sonoran	Low	yes	18.3	A-type	0.65	4.2	no
Ash-throated Flycatcher	Tyrannidae	Upper Sonoran	Low	no	28.0	A-type	6	4.3	no
Western Kingbird	Tyrannidae	Lower Sonoran	Low	no	37.9	other	3.7	3.78	no
Cassin's Vireo	Vireonidae	Transition	High	-	-	-	-	-	-
Warbling Vireo	Vireonidae	Transition	High	no	11.7	A-type	1.2	3.8	no
Steller's Jay	Corvidae	Transition	High	-	-	-	-	-	-
Western Scrub-Jay	Corvidae	Upper Sonoran	Low	yes	89.7	A-type	2.7	4.8	yes
Clark's Nutcracker	Corvidae	Hudsonian	High	yes	130	other	200	3.06	yes
American Crow	Corvidae	Lower Sonoran	Low	yes	506	other	1.25	4.7	yes
Common Raven	Corvidae	Upper	Low	yes	783	A-type	510	5.4	yes

		Sonoran							
Horned Lark	Alaudidae	Lower Sonoran	Low	yes	30.3	A-type	1.6	2.5	yes
Tree Swallow	Hirundinidae	Lower Sonoran	High	no	21.2	other	1600	5.4	no
Violet-green Swallow	Hirundinidae	Transition	High	-	-	-	-	-	-
Cliff Swallow	Hirundinidae	Upper Sonoran	Low	no	22.3	other	700	3.48	no
Mountain Chickadee	Paridae	Hudsonian	High	yes	11.7	other	6.47	7.05	no
Oak Titmouse	Paridae	Upper Sonoran	Low	yes	16.5	A-type	2.1	6.2	yes
Bushtit	Aegithalidae	Upper Sonoran	Low	yes	5.3	other	100	6.3	no
Red-breasted Nuthatch	Sittidae	Canadian	High	yes	10.5	other	2	5.8	no
White-breasted Nuthatch	Sittidae	Upper Sonoran	High	yes	21.1	A-type	12	7.3	no
Pygmy Nuthatch	Sittidae	Transition	High	yes	10.4	A-type	1	7.2	yes
Brown Creeper	Certhiidae	Transition	High	yes	8.4	A-type	0.5	4.9	no
Rock Wren	Troglodytidae	Upper Sonoran	High	yes	16.5	A-type	1.8	5.6	no
Canyon Wren	Troglodytidae	Upper Sonoran	Low	yes	11.3	A-type	18	5.1	no
Bewick's Wren	Troglodytidae	Upper Sonoran	Low	yes	9.61	A-type	2	5.6	no
House Wren	Troglodytidae	Upper Sonoran	Low	yes	10.6	A-type	0.93	6.6	no
Blue-gray Gnatcatcher	Polioptilidae	Upper Sonoran	Low	yes	5.7	A-type	1.8	4.35	no
American Dipper	Cinclidae	Canadian	High	yes	57.8	A-type	5	4.1	no
Golden-crowned Kinglet	Regulidae	Canadian	High	yes	6.2	A-type	1.6	7.4	no
Ruby-crowned Kinglet	Regulidae	Canadian	High	yes	6.7	A-type	2.9	7.64	no
Western Bluebird	Turdidae	Upper Sonoran	Low	yes	26.5	other	6	4.9	no
Mountain Bluebird	Turdidae	Hudsonian	High	yes	29.6	A-type	5	5.5	no
Townsend's Solitaire	Turdidae	Canadian	High	yes	32.5	other	15	4	yes
Hermit Thrush	Turdidae	Canadian	High	-	-	-	-	-	-
American Robin	Turdidae	Transition	High	yes	79.9	other	25	3.2	yes
Wrentit	Sylviidae	Upper Sonoran	Low	yes	14.8	A-type	0.62	3.6	no
Northern Mockingbird	Mimidae	Lower Sonoran	Low	yes	49.4	A-type	1.27	3.6	yes
Orange-crowned Warbler	Parulidae	Upper Sonoran	High	yes	9.3	A-type	0.32	4.6	no
Nashville Warbler	Parulidae	Transition	High	yes	8.8	other	1.1	4.71	no
Yellow Warbler	Parulidae	Transition	High	no	9.8	other	75	4.45	no
Yellow-rumped Warbler	Parulidae	Canadian	High	yes	12.1	other	0.8	3.86	no
Black-throated Gray Warbler	Parulidae	Transition	Low	-	-	-	-	-	-
Hermit Warbler	Parulidae	Canadian	High	no	10.4	A-type	0.35	4.3	yes
MacGillivray's Warbler	Parulidae	Transition	High	no	10.4	A-type	1.7	4.12	no
Common Yellowthroat	Parulidae	Lower Sonoran	Low	yes	10.1	A-type	0.71	4	no

Wilson's Warbler	Parulidae	Canadian	High	no	6.9	A-type	1.17	4.5	no
Yellow-breasted Chat	Incertae Sedis	Lower Sonoran	Low	no	25.1	A-type	1.2	3.26	yes
Green-tailed Towhee	Emberizidae	Canadian	High	yes	28.4	A-type	0.9	3.65	yes
Spotted Towhee	Emberizidae	Upper Sonoran	Low	-	-	-	-	-	-
California Towhee	Emberizidae	Upper Sonoran	Low	yes	55.6	A-type	4.8	3.69	yes
Chipping Sparrow	Emberizidae	Upper Sonoran	High	no	12.2	A-type	0.6	3.7	yes
Lark Sparrow	Emberizidae	Upper Sonoran	Low	yes	29.0	other	6	4.09	yes
Savannah Sparrow	Emberizidae	Transition	Low	yes	17.8	A-type	0.5	3.2	yes
Fox Sparrow	Emberizidae	Canadian	High	yes	32.5	A-type	0.6	3.24	yes
Song Sparrow	Emberizidae	Transition	High	yes	24.2	A-type	1	3.99	yes
Lincoln's Sparrow	Emberizidae	Canadian	High	yes	18.1	other	0.5	4.24	yes
White-crowned Sparrow	Emberizidae	Hudsonian	High	yes	26.9	A-type	0.15	4	yes
Dark-eyed Junco	Emberizidae	Canadian	High	yes	17.7	A-type	2.11	3.92	yes
Western Tanager	Thraupidae	Transition	High	no	30.1	A-type	2.83	3.4	yes
Black-headed Grosbeak	Cardinalidae	Upper Sonoran	Low	no	47.2	A-type	2.7	3.4	yes
Blue Grosbeak	Cardinalidae	Lower Sonoran	Low	no	27.0	A-type	6.1	3.62	yes
Lazuli Bunting	Cardinalidae	Upper Sonoran	Low	no	15.2	A-type	4	3.55	yes
Red-winged Blackbird	Icteridae	Lower Sonoran	High	yes	57.2	other	0.2	3.28	yes
Western Meadowlark	Icteridae	Lower Sonoran	Low	yes	97.7	A-type	3	5	no
Brewer's Blackbird	Icteridae	Upper Sonoran	High	yes	64.0	other	300	4.98	yes
Brown-headed Cowbird	Icteridae	Lower Sonoran	Low	yes	36.1	other	442	41	yes
Bullock's Oriole	Icteridae	Lower Sonoran	Low	no	33.6	other	13	4.94	yes
Purple Finch	Fringillidae	Transition	Low	-	-	-	-	-	-
Cassin's Finch	Fringillidae	Canadian	High	yes	27.6	other	6.4	4.4	yes
House Finch	Fringillidae	Lower Sonoran	Low	-	-	-	-	-	-
Red Crossbill	Fringillidae	Canadian	High	yes	33.4	other	80	3	yes
Pine Siskin	Fringillidae	Canadian	High	-	-	-	-	-	-
Lesser Goldfinch	Fringillidae	Upper Sonoran	Low	-	-	-	-	-	-
Lawrence's Goldfinch	Fringillidae	Upper Sonoran	Low	yes	10.2	other	110	4.86	no
American Goldfinch	Fringillidae	Lower Sonoran	Low	yes	11.9	other	300	5.2	no
Evening Grosbeak	Fringillidae	Canadian	High	yes	61.4	other	300	3.5	yes
House Sparrow	Passeridae	Lower Sonoran	Low	yes	28.5	other	700	5.14	no

Table S3. Avian shifts (m) of lower and upper range limits and range centers for elevational distributions in three Sierra Nevada regions. Dashes ('-') represent where a species did not have enough occurrences to be evaluated for a region.

English name	Scientific name	Northern			Central			Southern		
		Lower limit*	Range center†	Upper limit*	Lower limit	Range center	Upper limit	Lower limit	Range center	Upper limit
Mountain Quail	*Oreortyx pictus*	**-448**	**-214**	**-127**	0	41	300	-	-	-
California Quail	*Callipepla californica*	0	**59**	**539**	0	3	0	**-590**	0	0
Sooty Grouse	*Dendragapus fuliginosus*	-	-	-	347	28	-62	-	-	-
Band-tailed Pigeon	*Patagioenas fasciata*	-	-	-	**-632**	**130**	**821**	-	-	-
Mourning Dove	*Zenaida macroura*	0	**219**	**889**	0	**127**	**1266**	0	**142**	293
Black-chinned Hummingbird	*Archilochus alexandri*	-	-	-	-	-	-	-152	**-419**	**-1001**
Anna's Hummingbird	*Calypte anna*	-	-	-	**-523**	**149**	**987**	-	-	-
Calliope Hummingbird	*Stellula calliope*	0	**198**	488	467	**351**	**748**	-	-	-
Acorn Woodpecker	*Melanerpes formicivorus*	0	-11	**-448**	0	16	114	-	-	-
Williamson's Sapsucker	*Sphyrapicus thyroideus*	-	-	-	-104	-22	-386	0	-20	0
Red-breasted Sapsucker	*Sphyrapicus ruber*	**392**	37	678	**467**	19	0	**360**	26	654
Nuttall's Woodpecker	*Picoides nuttallii*	0	3	0	0	3	0	0	3	360
Downy Woodpecker	*Picoides pubescens*	0	11	**1244**	**-1155**	**-9**	0	-590	16	749
Hairy Woodpecker	*Picoides villosus*	**448**	3	**-279**	103	3	38	26	99	**-312**
White-headed Woodpecker	*Picoides albolarvatus*	**392**	32	34	**-467**	-44	**-362**	0	**26**	**447**
Northern Flicker	*Colaptes auratus*	24	-35	-63	0	-32	-21	**-590**	56	0
Pileated Woodpecker	*Dryocopus pileatus*	0	0	**-63**	**-114**	0	233	-	-	-
Olive-sided Flycatcher	*Contopus cooperi*	392	0	10	**-198**	3	**823**	-667	7	**951**
Western Wood-Pewee	*Contopus sordidulus*	0	11	0	-28	-25	**-386**	-590	-89	**-225**
Willow Flycatcher	*Empidonax traillii*	42	21	**218**	-	-	-	-	-	-
Hammond's Flycatcher	*Empidonax hammondii*	-392	**-72**	**-195**	0	**-89**	**-596**	-	-	-
Dusky Flycatcher	*Empidonax oberholseri*	0	24	214	15	38	**823**	0	23	15
Pacific-slope Flycatcher	*Empidonax difficilis*	-	-	-	-523	9	**482**	-	-	-
Black Phoebe	*Sayornis nigricans*	0	**123**	**538**	0	41	**1485**	-96	**-168**	-10
Ash-throated Flycatcher	*Myiarchus cinerascens*	0	-16	**-448**	0	**-108**	**-798**	77	-3	**-667**
Western Kingbird	*Tyrannus verticalis*	0	3	0	0	3	0	0	0	0
Cassin's Vireo	*Vireo cassinii*	**579**	**262**	0	0	**294**	**233**	-278	**-360**	**-512**
Warbling Vireo	*Vireo gilvus*	0	**182**	**-263**	0	13	**362**	-56	**327**	**742**
Steller's Jay	*Cyanocitta stelleri*	74	-3	214	0	0	-17	-389	0	**312**
Western Scrub-Jay	*Aphelocoma californica*	0	-21	**-448**	0	6	0	**-686**	-76	**-436**
Clark's Nutcracker	*Nucifraga columbiana*	-81	**75**	0	0	**57**	54	0	30	0
American Crow	*Corvus brachyrhynchos*	-	-	-	-	-	-	**-96**	10	0
Common Raven	*Corvus corax*	-	-	-	-	-	-	-68	**-205**	**225**
Horned Lark	*Eremophila*	-	-	-	-	-	-	**152**	**-49**	**-572**

	alpestris									
Tree Swallow	*Tachycineta bicolor*	0	64	19	-	-	-	-	-	-
Violet-green Swallow	*Tachycineta thalassina*	-13	3	98	0	3	-14	**-1586**	-16	**-549**
Cliff Swallow	*Petrochelidon pyrrhonota*	0	**-112**	**529**	-	-	-	-19	**-79**	0
Mountain Chickadee	*Poecile gambeli*	0	-8	0	0	-13	54	-389	-23	0
Oak Titmouse	*Baeolophus inornatus*	0	13	0	0	13	0	0	0	0
Bushtit	*Psaltriparus minimus*	0	8	**-228**	0	16	**1688**	**-590**	-16	**-389**
Red-breasted Nuthatch	*Sitta canadensis*	**-521**	**-110**	214	**-331**	-3	38	-158	-23	0
White-breasted Nuthatch	*Sitta carolinensis*	0	**134**	**-371**	0	**215**	**1003**	0	-96	0
Pygmy Nuthatch	*Sitta pygmaea*	-	-	-	-	-	-	0	43	-15
Brown Creeper	*Certhia americana*	0	3	279	**-331**	-13	75	**389**	-79	15
Rock Wren	*Salpinctes obsoletus*	79	-102	0	-495	**272**	92	26	**452**	0
Canyon Wren	*Catherpes mexicanus*	-	-	-	**-523**	-13	**890**	-	-	-
Bewick's Wren	*Thryomanes bewickii*	0	**206**	**477**	0	**203**	**545**	**-683**	**-703**	**-1567**
House Wren	*Troglodytes aedon*	24	96	0	**-523**	-6	**369**	-590	-59	**297**
Blue-gray Gnatcatcher	*Polioptila caerulea*	-	-	-	**523**	9	**331**	-	-	-
American Dipper	*Cinclus mexicanus*	392	**160**	**-272**	-	-	-	-	-	-
Golden-crowned Kinglet	*Regulus satrapa*	-126	-5	**-272**	0	0	206	-	-	-
Ruby-crowned Kinglet	*Regulus calendula*	-	-	-	**949**	**421**	0	**385**	**152**	15
Western Bluebird	*Sialia mexicana*	0	0	**137**	0	0	**-198**	-93	0	15
Mountain Bluebird	*Sialia currucoides*	**-67**	**72**	-10	-14	**25**	92	**486**	**132**	0
Townsend's Solitaire	*Myadestes townsendi*	**70**	0	10	**-188**	-3	0	-	-	-
Hermit Thrush	*Catharus guttatus*	**-126**	**-120**	**-263**	**467**	**117**	21	**-597**	7	0
American Robin	*Turdus migratorius*	-103	11	**214**	**-523**	**-142**	**461**	**-1416**	**-468**	15
Wrentit	*Chamaea fasciata*	-	-	-	0	0	**-331**	**-93**	0	0
Northern Mockingbird	*Mimus polyglottos*	-	-	-	-	-	-	**96**	**221**	**1213**
Orange-crowned Warbler	*Vermivora celata*	0	**-163**	**-127**	0	**142**	92	-	-	-
Nashville Warbler	*Vermivora ruficapilla*	0	-3	279	0	-13	-17	-	-	-
Yellow Warbler	*Dendroica petechia*	0	-75	0	0	-98	**-821**	-96	-73	**486**
Yellow-rumped Warbler (Audubon race)	*Dendroica coronata*	74	40	204	0	25	54	0	13	0
Black-throated Gray Warbler	*Dendroica nigrescens*	74	0	**-204**	**-198**	-3	**-280**	-	-	-
Hermit Warbler	*Dendroica occidentalis*	0	5	127	**-331**	-22	**-574**	-	-	-
MacGillivray's Warbler	*Oporornis tolmiei*	-448	**-118**	**-263**	**632**	**133**	233	-	-	-
Common Yellowthroat	*Geothlypis trichas*	24	**48**	**924**	-	-	-	**773**	**56**	0
Wilson's Warbler	*Wilsonia pusilla*	-24	**-438**	**-541**	0	**-411**	369	-19	**-1069**	**-653**
Yellow-breasted Chat	*Icteria virens*	37	**-214**	**-924**	0	**-171**	**-632**	-	-	-
Green-tailed Towhee	*Pipilo chlorurus*	**-56**	**51**	0	**452**	-3	**-845**	0	13	**-149**
Spotted Towhee	*Pipilo maculatus*	0	21	**529**	-28	38	**482**	0	36	**245**

California Towhee	*Pipilo crissalis*	0	0	0	0	0	0	**-686**	-3	**-667**
Chipping Sparrow	*Spizella passerina*	0	**414**	204	**1155**	**386**	38	**200**	**472**	0
Lark Sparrow	*Chondestes grammacus*	24	-21	70	-	-	-	0	53	**1321**
Savannah Sparrow	*Passerculus sandwichensis*	-	-	-	-	-	-	0	**1217**	**2503**
Fox Sparrow	*Passerella iliaca*	**448**	**195**	**692**	**-467**	**66**	**731**	0	**30**	**654**
Song Sparrow	*Melospiza melodia*	0	**174**	**406**	-	-	-	-19	**181**	**1273**
Lincoln's Sparrow	*Melospiza lincolnii*	**161**	5	10	-344	0	0	-	-	-
White-crowned Sparrow	*Zonotrichia leucophrys*	-	-	-	**570**	**165**	54	**-634**	**102**	0
Dark-Eyed Junco	*Junco hyemalis*	**521**	37	0	0	13	54	0	3	0
Western Tanager	*Piranga ludoviciana*	-43	-5	**-263**	0	-3	-14	0	-10	**-312**
Black-headed Grosbeak	*Pheucticus melanocephalus*	0	-11	**-233**	0	-6	0	-96	-3	**-523**
Blue Grosbeak	*Passerina caerulea*	-	-	-	-	-	-	-96	**-82**	**-251**
Lazuli Bunting	*Passerina amoena*	24	**-192**	**775**	-28	**133**	**890**	**696**	**1065**	**447**
Red-winged Blackbird	*Agelaius phoeniceus*	0	59	-79	0	**111**	**1416**	0	**148**	**2490**
Western Meadowlark	*Sturnella neglecta*	0	**-163**	**-223**	-	-	-	19	**-218**	**1321**
Brewer's Blackbird	*Euphagus cyanocephalus*	0	0	**410**	0	89	**509**	-133	-63	0
Brown-headed Cowbird	*Molothrus ater*	-	-	-	-	-	-	-96	**73**	1524
Bullock's Oriole	*Icterus bullockii*	0	**96**	0	0	**123**	**460**	0	69	0
Purple Finch	*Carpodacus purpureus*	-74	70	0	0	**592**	**1078**	**-825**	**-393**	**325**
Cassin's Finch	*Carpodacus cassinii*	**70**	**53**	214	**-681**	**-133**	92	**-245**	**-237**	225
House Finch	*Carpodacus mexicanus*	0	**174**	**977**	0	22	0	0	**-561**	**-1177**
Red Crossbill	*Loxia curvirostra*	-392	**179**	**-541**	-	-	-	-	-	-
Pine Siskin	*Spinus pinus*	**1003**	**286**	476	**570**	**174**	461	0	16	15
Lesser Goldfinch	*Spinus psaltria*	0	0	**-371**	0	-3	14	**184**	0	-143
Lawrence's Goldfinch	*Spinus lawrencei*	-	-	-	-	-	-	**667**	-10	15
American Goldfinch	*Spinus tristis*	0	**246**	**1316**	-	-	-	-	-	-
Evening Grosbeak	*Coccothraustes vespertinus*	**392**	**198**	488	**530**	**209**	534	-	-	-
House Sparrow	*Passer domesticus*	-	-	-	-	-	-	0	**112**	602

[*] Upper and Lower range boundary shifts presented in bold signify significant shifts with $P_{fa} < 0.05$ and magnitudes greater than 10% of the species' historic range. Non-significant shifts are in plain type while non-shifts (magnitude equal to 0) are presented as 0.

[†] Elevational center shifts measured directly from cumulative occupancy curves (see Methods). Values in bold represent ecologically significant shifts (magnitude of shift greater than 10% of species' historic range).

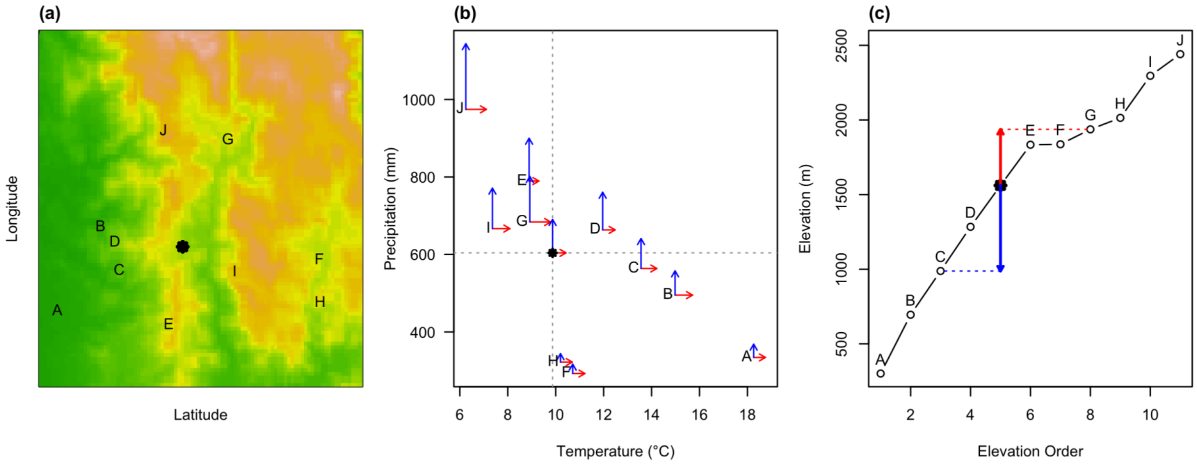
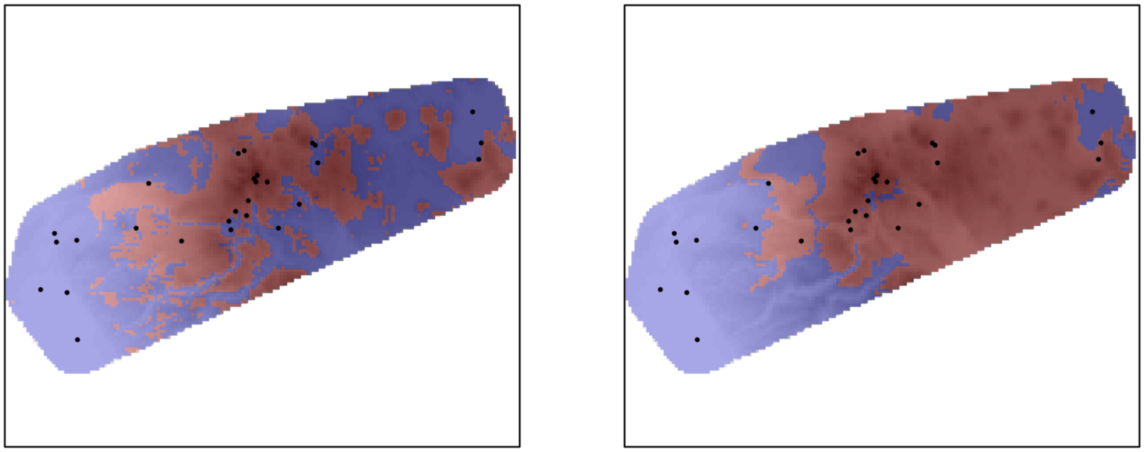
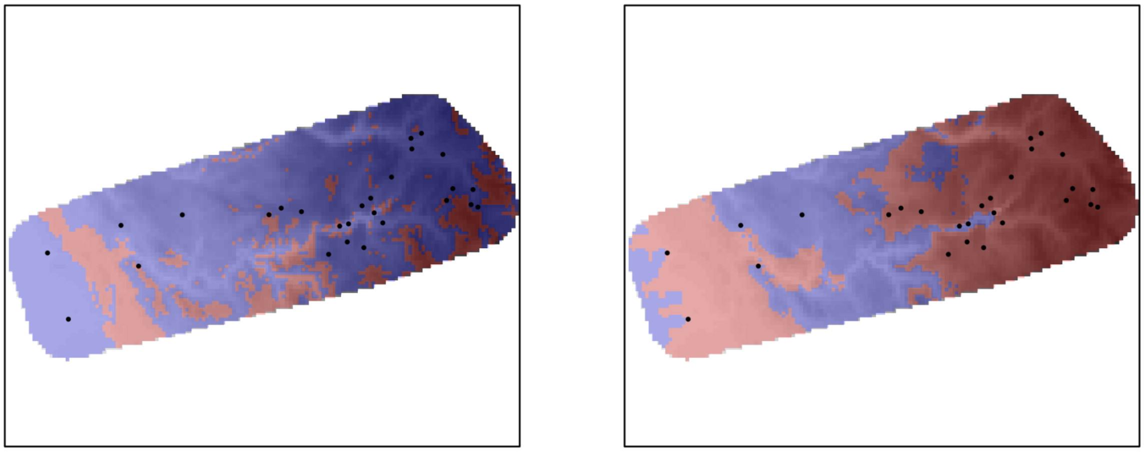


Figure S1. Schematic of how climatic nearest neighbors lead to predictions of elevational shifts. A hypothetical landscape (a) with topography as colored holds a focal site (star). The climate at the focal site is compared to the climate everywhere else in the region, here represented by 10 random points, labeled A-J. In climate space (b), each geographic location has a historical temperature and precipitation (the base of each arrow). Changes in climate over time are represented for each location separately for temperature (red arrows) and precipitation (blue arrows). Of interest is the geographic location which has a modern climate that is most similar to the historical climate of the focal site (dashed lines). The modern conditions of the focal site are different enough that it is no longer its own nearest climatic neighbor; rather, point G is the nearest temperature neighbor and point C is the nearest precipitation neighbor. Given the elevations of all sites (c), a species with a range limit at the focal site would be expected to shift upwards toward point G in order to most closely match its historical temperature conditions, while alternatively it would be expected to shift down toward points C in order to most closely match its historical precipitation conditions. Depending on the variability in climate in a region, temperature and precipitation may lead to the same or opposite predictions of elevational movement at a site.



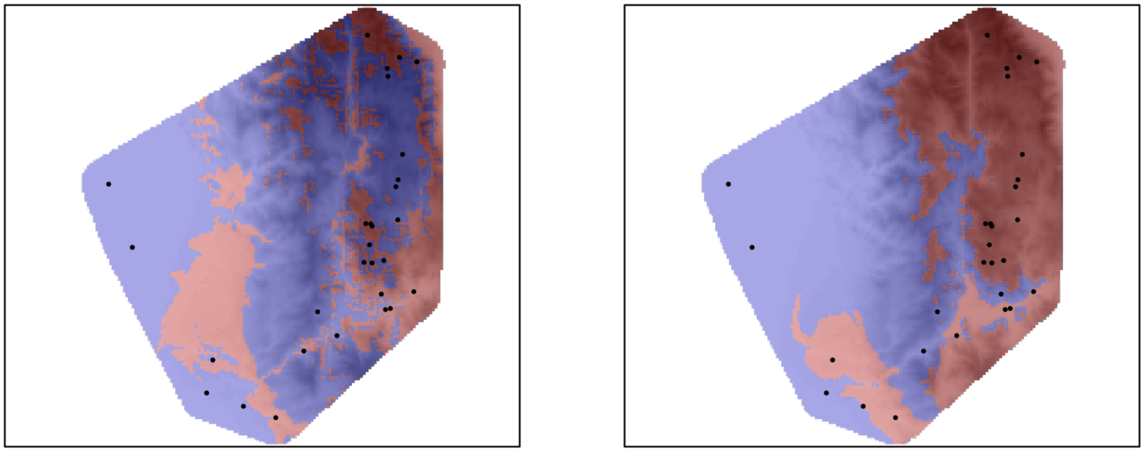
(a) Temperature (northern)

(b) Precipitation (northern)



(c) Temperature (central)

(d) Precipitation (central)



(e) Temperature (southern)

(f) Precipitation (southern)

Figure S2. The difference in elevation between grid cells and their nearest modern temperature (a, c, e) and precipitation (b, d, f) neighbors for each Sierra Nevada survey region (Northern: a-b;

Central, c-d; Southern, e-f). Differences are measured as whether the nearest modern climatic neighbor is higher in elevation (blue) or lower in elevation (red) than each grid cell. To calculate this, the average historic climate at each 1 x 1 km PRISM grid cell was compared to the average modern climate at all cells within each region (defined by a 10 km buffer around the convex polygon surrounding all survey sites), and the nearest 10% of cells were selected. The average elevation of these cells was compared to the elevation of the focal cell, resulting in cell-specific measures of nearest-neighbor elevational difference. These differences (red and blue shading) are shown on top of 1 x 1 km elevation (gray shading, darker is higher) along with survey point locations (black dots). As expected, based on climate change averages, most areas have temperature nearest neighbors at higher elevations. In the northern region (a), however, localized cooling at high elevations results in nearest temperature neighbors at lower elevations for those areas. Precipitation patterns show markedly different patterns, with low to middle elevation areas having nearest neighbors higher up, and high elevation areas having nearest neighbors lower down.

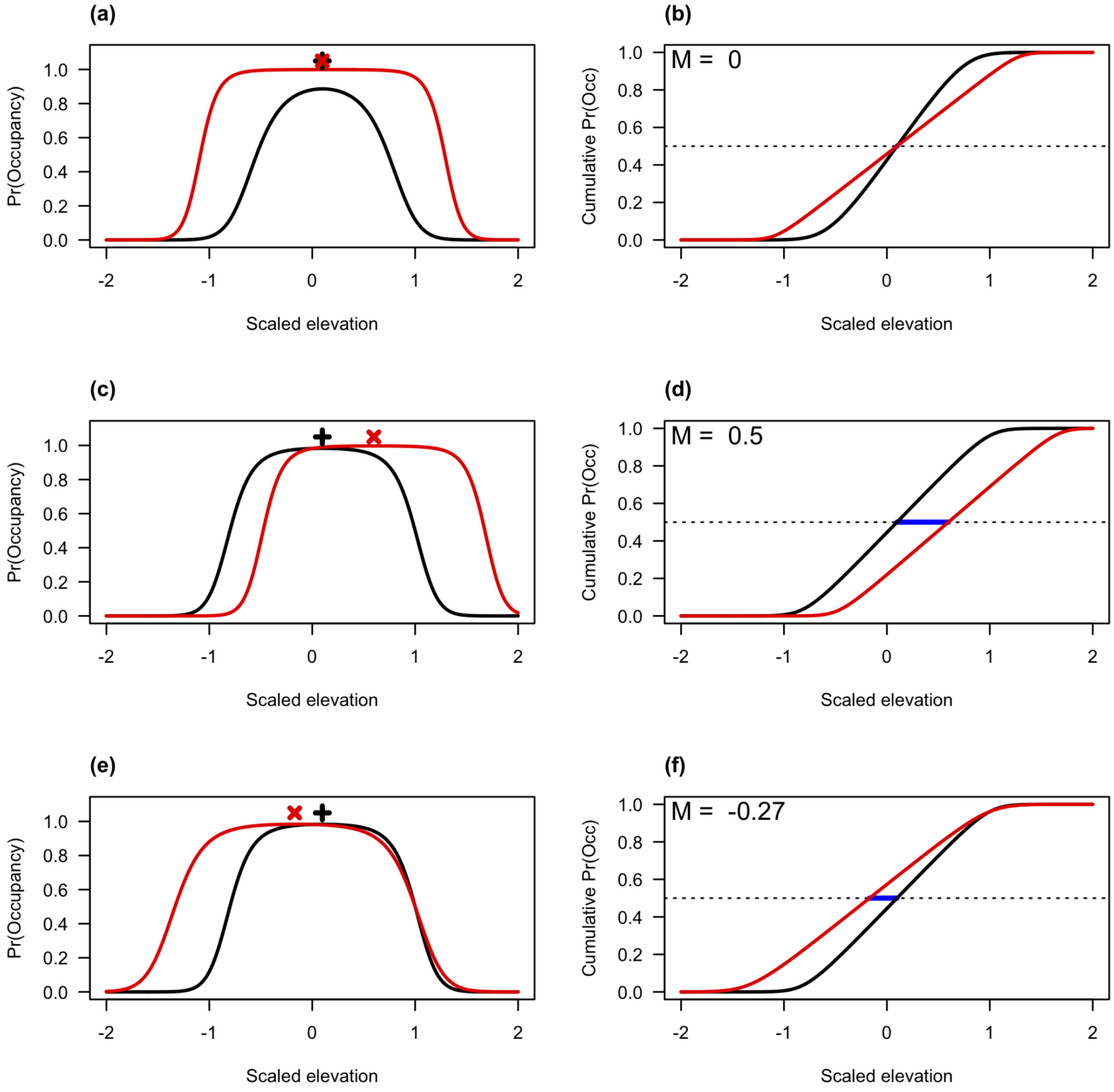


Figure S3. Hypothetical elevational ranges (a, c, e) showing different patterns of range change over time and how the range center, as estimated from cumulative probability of occupancy curves (b, d, f), describes these shifts. For each occupancy plot with elevation (a, c, e), both historical (black) and modern (red) occupancy curves are depicted along with the estimated range centers for each time period (historical = black "+", modern = red "x"). Range centers are calculated by graphing occupancy probability as a cumulative curve from the lowest surveyed elevation to the highest surveyed elevation, and finding the point where occupancy probability is equally distributed above and below. When cumulative occupancy is scaled to sum to 1 (as depicted here), the range center will be the elevation at which the cumulative curve equals 0.5. The difference between range centers is highlighted in blue, and quantified by the value "M" in the corner of each graph. While the magnitude of M is scale-dependent, the sign of M signals the direction of shift. When range limits expand equally upwards and downwards (a), the range center will not change (b). If both limits increase in elevation (c), the range center will also increase (d). If only one limit shifts, for example if the lower limit decreases in elevation (e), then the range center will shift in that same direction (f).

Chapter 4.

Cryptic loss of montane avian richness over 100 years

Abstract

Of critical importance to conservation is the impact of climate change – past and future – on global species diversity. Few studies have investigated how diversity has changed with climate change using empirical data derived over long time spans, and none have done so while fully accounting for changes in species-specific detectability over time. This study uses bird surveys collected 80-100 years apart over three elevational gradients in the Sierra Nevada of California, USA to examine long-term changes in richness and species turnover. Occurrence data were analyzed using a hierarchical Bayesian occupancy model to account for species and survey-specific detectability of 210 bird species. Richness broadly declined over the 20th century across all elevations, indicating individual species' had contracted their ranges more often than expanding them. Turnover was greatest at the highest and the lowest elevations. These findings were only apparent after species detectability was incorporated into measures of species diversity. Partitioning of species richness changes by elevational life zone showed that diversity of high-elevation species declined, without a concurrent expansion by mid-elevation species. These 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.

Introduction

Assessing change in species diversity is critical to understanding the long-term community-level impacts of climate change. Although climate change has resulted in species moving up in elevation and poleward in latitude (Parmesan and Yohe 2003, Root et al. 2003), generalized empirical patterns of climate-induced changes in species richness along elevational or latitudinal gradients are lacking (Böhning-Gaese and Lemoine 2004). Most studies have examined range shifts of individual species (Parmesan and Yohe 2003, Root et al. 2003), thereby inferring changes to richness based on an incomplete sampling of the species pool. Predictions of future responses for entire communities include putative substantial losses of species diversity (Peterson et al. 2002, 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, La Sorte and Jetz 2010).

Despite long-term predictions of diversity loss, evidence for declines in species diversity from climate change has been equivocal. This is particularly true of studies along elevational gradients. Recent studies of climate change impacts on montane regions have documented species richness declines across elevation (Wilson et al. 2007, Moritz et al. 2008), increases across elevation (Grabherr et al. 1994, Popy et al. 2010), and declines at low elevation but increases at high elevation (Forister et al. 2010). This lack of uniform empirical observations on richness may be partially due to the imperfect detection of species that can bias measures of richness and community structure (Boulinier et al. 1998, Kery and Royle 2008, Popy et al. 2010). Since detectability differences between observers are expected to widen over time due to changing methods, technology, and knowledge of identification (Tingley and Beissinger 2009), it is critical that empirical studies of richness change account for these differences.

This study uses unbiased estimators of species richness that incorporate detectability to explore how bird species richness and turnover have changed across elevation in the Sierra Nevada mountains given nearly a century of climate change. Previous research on birds in the Sierra Nevada has illustrated how temperature and precipitation changes during the last century have led to range shifts for individual species (Tingley et al. 2009; Chapter 3). Community changes are the cumulative consequence of individual range shifts (Menéndez et al. 2006). By examining the ranges of all species in a region, the overall impact of climate change on species richness and turnover can be evaluated.

We present a framework for climate warming impacts on species richness along an elevational gradient (Figure 1) that presents testable hypotheses for how species richness and composition could change over time. Species richness is generally greatest at mid-elevations (Lomolino 2001, McCain 2009). If species respond uniformly to climate change within their elevational range (Wilson et al. 2005), species richness along elevational gradients can be expected either to increase or decrease across all sites (Figure 1B, “Broad Shift” model). Long-term projections of climate change impacts (e.g., Thomas et al. 2004, Jetz et al. 2007) suggest that richness should decrease along elevational gradients, although in the short-term extinctions may lag behind colonizations, leading to richness increases (Walther et al. 2002, Menéndez et al. 2006). In contrast, if species shift together as a community, with colonizations at upper limits and extinctions at lower limits, the form of richness with elevation may simply be translated to higher elevations (Figure 1C, “Translation” model). Finally, if species respond differently across the elevational gradient, for example due to differing colonization abilities or extinction lags, richness changes may only be detectable at elevational extremes (Figure 1D, “Edge Shift” model; Forister et al. 2010). Compared to richness, species turnover over time at a site is predicted to be greatest at middle elevations (Stralberg et al. 2009), where low elevation species shift up and replace mid to high elevation species. This leads to a non-linear response of turnover to elevation, with an expected convex hump at middle elevations.

Methods

Study sites and bird surveys

Survey sites were distributed across three elevational cross-sections of the Sierra Nevada and southern Cascade mountains of eastern California, U.S.A (Chapter 3). This area has seen significant anthropogenic-induced climate warming over the last 80 years (Bonfils et al. 2008a). A total of 84 sites were surveyed for birds between 2003-2009 (Tingley et al. 2009; Chapter 3), of which 77 were matched to historic survey routes visited repeatedly between 1911-1929 by researchers from the Museum of Vertebrate Zoology (MVZ) at UC Berkeley. Survey sites ranged in latitude (35.325° N to 40.647° N), longitude (122.219° W to 118.140° W), and elevation (61 m to 3,356 m), and represented the full array of Sierran vegetation-based life zones. Sites were located primarily in protected areas, minimizing potential land use interactions. In rare instances (n=5) where historical sites were partly or mostly converted to habitats that differed from original conditions, proxy sites within 1 km and containing the originally-described habitat composition were surveyed instead.

Historical bird surveys were conducted by Joseph Grinnell and other zoologists as part of field expeditions throughout the state of California in the early 1900s. The surveys followed line transects, and were often repeated at daily intervals, with a maximum of 17 visits (median = 3). Abundance data were not collected using standardized, reliable methods, but all species encountered were listed, providing detection/non-detection data. Locations, bird lists, and relevant metadata were extracted from historical field notes archived within the Museum of Vertebrate Zoology at the University of California, Berkeley (and available online at http://bscit.berkeley.edu/mvz/volumes.html).

Modern bird surveys were conducted as part of a systematic multi-taxon resurvey of the work by Grinnell and others, as described elsewhere (Moritz et al. 2008, Tingley et al. 2009). Six primary observers conducted point counts following, as best as possible, the same routes taken by historical surveyors, using variable-distance point counts (Ralph et al. 1995) lasting seven minutes. Point count stations were separated by a minimum of 250 m and placed along the full extent of the historical route, resulting in transects that varied in length (median of 10 points over 2.5 km). Sites were resurveyed repeatedly, often on successive days, with a maximum of 5 visits (median = 3).

Bird observations were limited to those that characterized breeding communities. Historical surveys were conducted between late March-early October, with most taking place between May-August. Modern surveys were entirely conducted between May-August. Individual birds identified as either juveniles or migrants were excluded from analysis.

Latitude-adjusted Elevation

Along latitudinally-oriented mountain ranges, animals and plants in the north of the range hold different elevational ranges than the same species do in the south of their range (Merriam 1894, Grinnell 1917a). The rate at which elevational communities change with latitude is ultimately determined by the rate at which temperature varies with elevation (lapse rate) and the rate at which temperature varies with latitude (meriodonal gradient), yet empirical rates can differ by taxon (e.g., Cogbill and White 1991, Lambert et al. 2005) and geographic region (Diaz and Bradley 1997). In order to compare richness across three sampled elevational gradients, an elevation standardization was needed. 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 modeled as a decline of 130.1 m per increase of 1° latitude. We used this rate to adjust elevations of all survey sites, standardizing them to a latitude of 35.3° N (the southern-most site).

Life Zone Classifications

Species were categorized *a priori* into life zone groups based on classifications of their historical Sierra Nevada breeding ranges in 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, Upper Sonoran, Transition, Canadian, Hudsonian, and Alpine/Arctic. Based on his years of observations, Grinnell provided estimates of the lowest, highest, and optimal life zone occupied for each bird species discussed. The optimal life zone was used as categorization for this study. Species that were detected in surveys yet not classified by Grinnell were lumped into a single "unclassified" category. As only one species, Gray-crowned Rosy-Finch (*Leucosticte tephrocotis*), was classified as Alpine, life zone specific results are not presented for this zone.

Multi-species Occupancy Model Estimation of Species Richness

Multi-species occupancy models (Dorazio and Royle 2005) implement individual species' models of occurrence within a hierarchical (i.e., multi-level) 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 (Russell et al. 2009, Zipkin et al. 2009, Zipkin et al. 2010). Although true community properties in nature cannot be known with certainty, these methods produce results at least as unbiased as previous methods (Kery and Royle 2008) while also accounting for detection heterogeneity.

Multi-species 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 mean and variance. By relating all species through the hierarchical component, inference can be made on species with low numbers of detections that otherwise may be difficult or impossible to model on their own (Link and Sauer 1996, Russell et al. 2009). Hierarchical models estimate the probability of occupancy of every species without *a priori* assumptions of how species should co-occur, allowing estimation of community descriptors that depend on having data for all species (Zipkin et al. 2009).

In our model, sites were modeled as unlinked in an 'unpaired-site' framework (Tingley and Beissinger 2009). We combined historical paired sites (n=77), modern paired sites (n=77), and modern unpaired sites (n=7) in a "single-season" occupancy approach (MacKenzie et al. 2003, MacKenzie et al. 2006) where occupancy for all sites in both time periods (n=161) was modeled simultaneously. By allowing occupancy to vary by survey era, this parameterization deactivates the structural autocorrelation between the probability of occurrence of a species at a site in the first time period and the probability of occurrence of the species at the same site in the second time period. Adding unpaired sites into the analysis strengthens the relationship between occupancy and elevation (Moritz et al. 2008, Tingley and Beissinger 2009).

We developed a multi-species hierarchical community model based on survey-specific detection/non-detection records to estimate species-specific occupancy status and community metrics (for paired sites only) in each survey era. Observed data, y_{ijk}, for species $i = 1,2,\ldots,210$ at site $j = 1,2,\ldots,161$ on survey day $k = 1,2,\ldots,17$ were modeled as resulting from the imperfect observation of a true occurrence state, z_{ij}, given a probability of detection, p_{ijk}. This observation process was modeled as, $y_{ijk} \sim \text{Bern}(p_{ijk} \cdot z_{ij})$, where $z_{ij} = 1$ if species i was truly present at site j, and $z_{ij} = 0$ if species i was not present at site j.

In the model, true occurrence is a Bernoulli-distributed outcome of the probability of occupancy by a species at a site. However, following Kéry and Royle (2008), the observed dataset for N = 210 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, $z_{ij} \sim \text{Bern}(\psi_{ij} \cdot w_i)$, where ψ_{ij} 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 $w_i \sim \text{Bern}(\Omega)$. For more information on data-augmentation, see Dorazio & Royle (2005), Dorazio et al. (2006), and Royle and Dorazio (2008). It is important to note that these unobserved species are not included in site-specific estimates of species richness dependent on covariate relationships.

Consistent with single-species approaches to occupancy modeling (e.g., MacKenzie et al. 2006), 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. 2009), two covariates were chosen to describe detectability: the era in which the survey was conducted (*era*) and the linear and quadratic effect of season (*jday*), as defined by Julian day (i.e., January 1st = 1). The probability of detection was modeled as follows, where $\alpha_{0\ldots3,i}$ are model coefficients for detectability:

$$\text{logit}\left(p_{i,j,k}\right) = \alpha_{0,i} + \alpha_{1,i} era_j + \alpha_{2,i} jday_{j,k} + \alpha_{3,i} jday_{j,k}^2$$

Expanding on the single-species model used by Moritz et al. (2008), occupancy was modeled as a linear function of three covariates: the 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 $\beta_{0\ldots7,i}$ are species-specific model coefficients for occupancy:

$$\begin{aligned}\text{logit}\left(\psi_{i,j}\right) = {} & \beta_{0,i} + \beta_{1,i} era_j + \beta_{2,i} elev_j + \beta_{3,i} elev_j^2 + \beta_{4,i} era_j elev_j + \beta_{5,i} era_j elev_j^2 \\ & + \beta_{6,i} R1_j + \beta_{7,i} R2_j\end{aligned}$$

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 parameters can be easily calculated from posterior draws of Markov chain Monte Carlo (MCMC) runs, propagating 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

$$N_j = \sum_{i=1}^{210} z_{i,j}$$

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 zone, such that

$$N_{j,\lambda} = \sum_{i=1}^{210} z_{i,j}\lambda_i$$

where the site-specific richness for a given life zone, $N_{j,\lambda}$, is a function of the species truly present ($z_{i,j}$) and whether each species was a member of the life zone (λ_i).

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

$$T_c = 1 - \frac{2 \cdot \sum_{i=1}^{210} z_{i,j=c_a} \cdot z_{i,j=c_b}}{N_{j=c_a} + N_{j=c_b}}$$

for paired 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 (R Development Core Team 2010) using the package 'R2WinBUGS' (Sturtz et al. 2005). Uninformative priors were used for means and variances of the hyper-parameters. The full model specification can be seen in Appendix S1. We ran three parallel chains of length 30,000, discarding the first 20,000 as burn-in, and with a thinning rate of 10. This resulted in a posterior distribution consisting of 3,000 samples for each parameter. Convergence was assessed using the Gelman-Rubin diagnostic (Gelman et al. 2004). Posterior means for occupancy parameters ($\beta_0 - \beta_7$) are included in Table S1. All means are given as ± standard error, unless otherwise noted.

Testing hypothetical models of richness change

Richness changes over time for all species and for species in each life zone grouping were evaluated with respect to four hypothetical models of change patterns (Figure 1). For each species assemblage, a general linear model for richness (posterior means for each site) was initially fit using a model including elevation (linear and quadratic terms), survey era, and interactions between era and elevation (linear and quadratic). This "full" model corresponded to the model for the "Edge Shift" hypothesis (Figure 1d). Likelihood ratio tests were subsequently used to determine the best hypothesis, following a stepwise progression from the full model to the “No Change” model (elevation and elevation^2 only). Simpler, nested models were determined to have no significant loss of explanatory power if the likelihood ratio test provided a $P > 0.05$.

Results

Species richness and turnover

Bird species richness decreased across the full elevational gradient in the Sierra Nevada over the 21st century when accounting for unobserved species at sites (Figure 2a). A total of 35 sites (45%) had modern species richness significantly less than historical estimates (i.e., 95% credible intervals non-overlapping with posterior means). An additional 25 sites (32%) showed no significant change over time, while the remaining 17 sites (22%) gained a significant number of species. Sites with significantly lower richness were dispersed across the entire elevational gradient, while 8 of 17 sites with significantly higher richness were clustered between adjusted elevations of 2300-2600 m (Figure 3). Significant declines in estimated richness ranged from 2.7 to 15.5 species (median = 7.2).

A general linear model predicting posterior means of site richness as a function of elevation and era was used to test whether the richness curve changed over time. Neither the interaction between era and elevation^2 (Likelihood ratio test: $P = 0.388$) or era and elevation (Likelihood ratio test: $P = 0.985$) contributed significantly to model performance. Subsequently, in the best-supported model, richness had a quadratic relationship with elevation, with peak richness at 779 m (elevational equivalent at 35°N), and the shape of the curve did not change over time (Table 1). However, the majority of sites significantly decreased in richness (Figure 3); across all elevations, richness decreased by an average of 2.0 ± 0.9 species per site over the 21st century (Table 1). Without significant interactions between elevation and era in describing richness, the results best support the hypothesis that richness has changed equally across all elevations (i.e., the Broad Shift model, Figure 1b).

Species turnover indicated that while richness broadly decreased by two species per site, an even greater number of species become locally extinct at sites and were replaced by colonizing species (Figure 4). Community turnover at sites over time ranged between 16% and 56% (median = 35%). Along the elevational gradient, temporal turnover showed a quadratic form with greatest turnover at the extremes of the elevational gradient (Figure 4). While this quadratic shape was statistically significantly (Likelihood ratio test on quadratic model versus linear model: $P < 0.001$), the effect was small (coefficient of elevation^2 term: -0.029 ± 0.007 s.e.), resulting in a very shallow change in turnover with elevation (Figure 4). Thus, while species richness may have decreased uniformly (Broad Shift model), compositional changes were biased toward elevational extremes, which could result from proportionally greater change in species composition at high and low elevations (either Edge Shift or Translation models).

Species-specific contributions to richness

Species in the lowest and highest life zones – Lower Sonoran, Canadian, and Hudsonian (Table 1) – showed the greatest changes in richness over the last 100 years (Figure 5). Almost 40% of sites had significantly fewer Lower Sonoran species when revisited, and these sites were clustered toward low elevations (Figure 5a). A linear model of Lower Sonoran species richness indicates that richness significantly decreased over time at low elevations (Table 1), supporting an Edge Shift pattern. Similarly, 65% of sites had significantly more Hudsonian species historically, with the greatest departures at high elevations (Figure 5e), thus describing a Translation model. Hudsonian richness significantly declined by about 0.5 species per site over the entire elevational gradient, although these declines were significantly greater at high elevations (Table 1). Canadian zone species richness showed significant declines across the gradient (Figure 5d), with an average loss of 1.2 species per site over time (Table 1). This followed a Broad Shift model.

Species unclassified into life zones by Grinnell showed a different pattern from the classified species and significantly increased over time at 35% of sites. These sites were distributed across the elevational gradient, but unclassified species richness only increased significantly at low elevations (Figure 5f, Table 1), following an Edge Shift model. Unclassified species (see Table S1 for species list) included species that breed in or near the Sierra Nevada but which are confined to specific habitats; for instance, 19 of 40 unclassified species are "waterbirds" associated with aquatic habitats such as lakes or rivers. The remaining 21 species consisted of those that (1) were introduced to California over the last century; (2) naturally expanded their range into California or the Sierra Nevada; (3) were more prominent components of other regions' avifauna yet which occur in limited parts of the survey region; and (4) were broadly and infrequently distributed with no obvious life zone. Unclassified species were not unique to modern resurveys; 40% of unclassified species were detected in at least one survey historically.

Consequences of imperfect detectability

Imperfect detection of species substantially biased the results and interpretation of richness change and turnover over time. The mean probability of detection differed markedly between the historical and modern surveys (Figure S1). For a single survey in the middle of the breeding season, the mean probability of detection for a species historically was 0.37 (95% CI: 0.35 – 0.39), while the mean modern probability of detection was 0.61 (95% CI: 0.59 - 0.64). On a species-by-species basis, detectability was significantly higher in modern surveys than historical ones (paired t-test: $n = 210$, $t = -29.7$, $P < 0.001$).

Differences in detectability over time led to differing counts of per-site species richness based on observed species versus estimated true richness (Figure 2). After accounting for undetected species, the richness of the average historical site increased by 17.0 species and the richness of the average modern site increased by 5.3 species. This difference led directly to divergent interpretations of richness trends over time. Not accounting for imperfect detection yielded a significant gain in observed richness over time (era coef ± s.e. = 9.48 ± 1.51; $P < 0.001$), in stark contrast to the significant decrease in richness that we found once detectability was incorporated (Figure 2). The substantial difference in interpretation is particularly clear at the scale of the individual survey site (Figure 3).

While accounting for detectability increased estimates of species richness at both historic and modern sites, it also generally decreased turnover in avian communities between paired sites (Figure 4). Turnover decreased for all 35 sites that showed significant differences in turnover between naïve and detection-based estimates (Figure 4). While community turnover estimated without incorporating detectability also showed a significant quadratic effect with elevation (with turnover greatest at elevational extremes), the quadratic effect was twice as strong as when accounting for unobserved species (coefficient of elevation^2 term for naïve analysis: -0.059 ± 0.014 s.e).

Discussion

Bird communities along an elevational gradient in the Sierra Nevada showed a great degree of change over the last century. While per-site species richness significantly declined over time, with some sites showing net losses up to 15 species, the average site only lost two species. While the loss of two species may be small relative to average richness at a site (n=46), sites on average experienced a 35% turnover in their species pool, indicating a high degree of underlying change in 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

It has been well demonstrated that many taxa show humped or declining patterns of species richness along elevational gradients (Rahbek 1997, Lomolino 2001, McCain 2009), and that the pattern can change depending on the resolution of elevational bands (Nogués-Bravo et al. 2008). This study found bird richness followed a quadratic, or humped pattern, although the maximum richness was located relatively close to the bottom of the gradient (Figure 2). There was no statistical evidence that the form of the richness curve changed over time (e.g. Figure 1d), as can happen when low-elevation areas experience greater levels of land-use change and modification than high elevation areas (Nogués-Bravo et al. 2008). Nor was there evidence of a translation of the richness curve, which would be expected if all species shifted equally upslope (Wilson et al. 2007) (Figure 1c). Rather, richness equally decreased across the entire elevational gradient, indicating relatively equal declines (Figure 1b).

Turnover in bird species composition in the Sierra Nevada over the past 100 years showed an unexpected relationship with elevation. Based on predictive work (Stralberg et al. 2009), species shifting upward with climate warming were expected to cause the greatest turnover at middle elevations where distinct elevational communities replace each other. Our results indicate that turnover in this study area was greatest at the lowest and highest elevations (Figure 4), although the strength of the pattern is debatable. The potential reasons for this pattern can be explained by examining the richness changes of birds in each life zone individually (Figure 5). 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-dominated landscape (La Sorte and Boecklen 2005). In the case of waterbirds, the anthropogenic altering of historical water regimes has led to increases in summertime availability of water in irrigated areas of California's Central Valley. High elevation areas (>2500 m), meanwhile, 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. A few elevational bands did experience increases in richness (Figure 3), particularly between 2300-2600 m. This region had large, localized, increases in richness of Transition zone species (Figure 5c), which may indicate the upwards colonization of multiple species characteristic of that life zone. Similarly, the upslope colonization of species has led to increased richness of butterflies at high elevations in the Sierra Nevada (Forister et al. 2010).

Our results agree with previous work showing broad-scale declines in richness over time (e.g., Wilson et al. 2007, Moritz et al. 2008), yet they demonstrate that richness shifts result from a high degree of underlying community dynamics. The failure to detect significant changes in the form of the richness curve over time indicates 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 species individualistically tracking different climatic parameters through time (Tingley et al. 2009). This has resulted in some species responding to climate change by shifting up, while other species of the same elevational zone shifted down (Chapter 3). An overall decline in species richness indicates that these individualistic range shifts are cumulatively resulting in range contractions more often than range expansions. This was confirmed by an independent analysis of range limit changes of individual species (M. Tingley, unpublished data).

Causes of change in species richness

The attribution of long-term community change through the analysis of occurrence datasets is hindered by a number of external 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 (Wiens 1981, Holmes et al. 1986). Additionally, richness is related to the magnitude of the area surveyed (Rahbek 1997) and survey effort (White et al. 2006, Magurran et al. 2010). Consequently, comparing single snapshots of communities, even within a year, can result in high estimates of turnover (Wiens 1981, Maron et al. 2005).

Our results are robust to these potential biases. Foremost, these 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 as found (Figures 2, 3). While we are unaware of studies of annual turnover in bird communities of the Sierra Nevada, the North American Breeding Bird Survey in the eastern United States found annual turnover to be well below 10% (Boulinier et al. 2001). The present finding of an average site turnover of 35% over 80-100 years indicates that species composition has likely changed far beyond that due to natural annual turnover. This result is similar to the long-term outcome described as a "shifting baseline" of community structure (Rittenhouse et al. 2010).

Finally, a large number of factors can result in changes to community composition, and a single attribution to climate change of all changes is implausible. Different habitats can have different rates of background turnover (Magurran et al. 2010); thus, the observed relationship of turnover with elevation may be biased by the change in habitat as elevation increases. Additionally, land use change and habitat shifts are likely to cause species turnover and richness shifts (Yahner 1997, Boulinier et al. 2001). In the Sierra Nevada, land-use change has been relegated mostly to 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. However, forest compositions at all elevations have 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 Ponderosa Pine *Pinus ponderosa* (Thorne et al. 2008). However, this tree species is most characteristic of the Transition life zone (Hall and Grinnell 1919), which exhibited a stable bird community over time (Figure 5c). While no study should be expected to show full attribution of results to climate change (Parmesan et al. 2011), when examining cumulatively the observed relationships between 20th century shifts in bird species ranges (Tingley et al. 2009, Chapter 3), the resultant declines in richness and turnover in species, especially at high elevations, 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 be a major confounding effect of long-term studies of species occurrence. In this study, detectability of bird species was shown to substantially increase over a century. Analyses accounting for detectability demonstrated a hidden decrease in richness, while those that did not indicated an increase in richness over time and a skewed functional relationship of turnover with elevation. While the difference in detectability observed over time in this study may be high, 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 5 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 of species richness have done so. Trends from observed data showing richness declines, even when non-parametric richness estimators are used (e.g., 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.

Table 1. Parameter estimates for results of linear models explaining estimated true species richness as a function of survey era, elevation (linear and quadratic effects) and interactions between the two. Results are shown for total species richness, and richness of particular life zones. Best models were selected by likelihood ratio tests using backward steps from the initial full model (larger model kept if $P < 0.05$). Parameter significance (coefficient t-tests) is indicated by asterisks (* = $0.05 < P < 0.01$; ** = $0.01 < P < 0.001$; *** = $P < 0.001$). Based on the significant effects for each species grouping model, the pattern of changes in species richness was assigned to a model class, as defined by Figure 1.

	Best model class	Intercept	Era	Elevation†	Elevation^2	Era*Elev.	Era*Elev.^{2}
All species	Broad Shift	51.56 ± 0.84 ***	-1.99 ± 0.93 *	-9.69 ± 0.49 ***	-4.06 ± 0.47 ***	-	-
Life zone groups							
Lower Sonoran	Edge Shift	2.75 ± 0.31 ***	0.45 ± 0.43	-4.63 ± 0.22 ***	2.22 ± 0.21 ***	0.66 ± 0.31 *	-0.84 ± 0.30 **
Upper Sonoran	No Change	14.40 ± 0.43 ***	-	-7.98 ± 0.41 ***	-	-	-
Transition	No Change	15.96 ± 0.34 ***	-	-2.00 ± 0.24 ***	-4.12 ± 0.23 ***	-	-
Canadian	Broad Shift	14.81 ± 0.49 ***	-1.24 ± 0.55 *	3.55 ± 0.29 ***	-2.81 ± 0.28 ***	-	-
Hudsonian	Translation	2.40 ± 0.12 ***	-0.54 ± 0.13 ***	2.10 ± 0.09 ***	0.32 ± 0.07 ***	-0.38 ± 0.12 **	-
Unclassified	Edge Shift	0.56 ± 0.19 **	-0.08 ± 0.27	-0.67 ± 0.13 ***	0.56 ± 0.13 ***	-0.26 ± 0.19	0.77 ± 0.18 ***

† Elevation was centered and scaled to a standard deviation of 1 prior to modeling. Thus, an increase in scaled elevation of 1 unit is equal to a true elevation increase of 950 m.

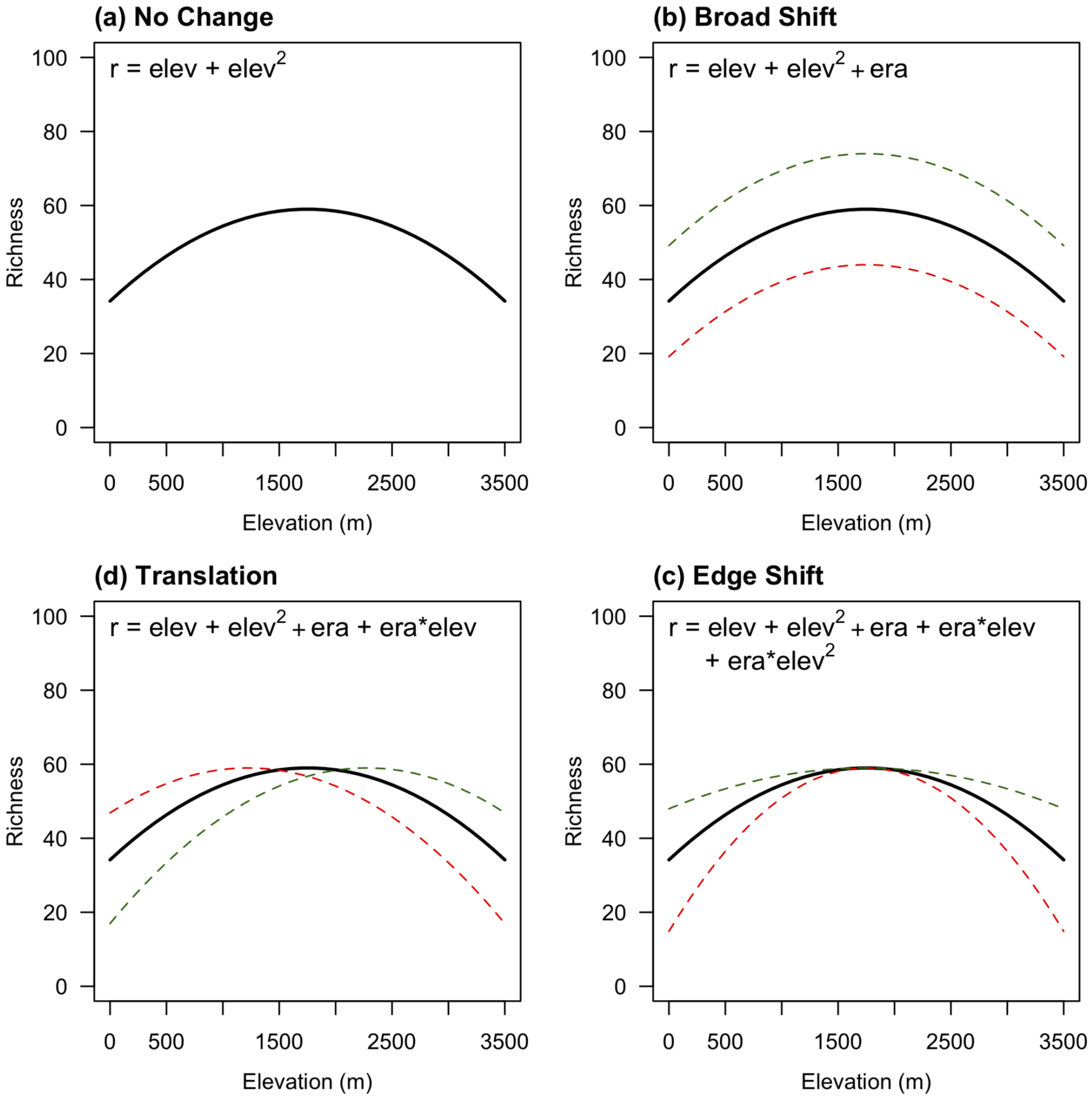


Figure 1. Hypothesized changes of species richness over time along an elevational gradient. As a null model, species richness may not differ between time periods (a, "No Change"). However, widespread extinctions or colonizations at sites can lead richness to increase (green dashed line) or decrease (red dashed line) uniformly over time across all elevations (b, "Broad Shift"). If all species shift uniformly as one community, then the richness curve should be translated on elevation, resulting in richness shifts throughout the elevational range, but with opposite richess trends at elevational limits (c, "Translation"). Finally, communities at elevational extremes may be most likely to gain or lose new members as species immigrate or emigrate, resulting in richness shifts, matching in direction, at only those elevations at the limits of the gradient (d, "Edge Shift"). Each model for richness ("r") can be empirically tested using general linear models on site-specific richness data (model equations shown within each graph).

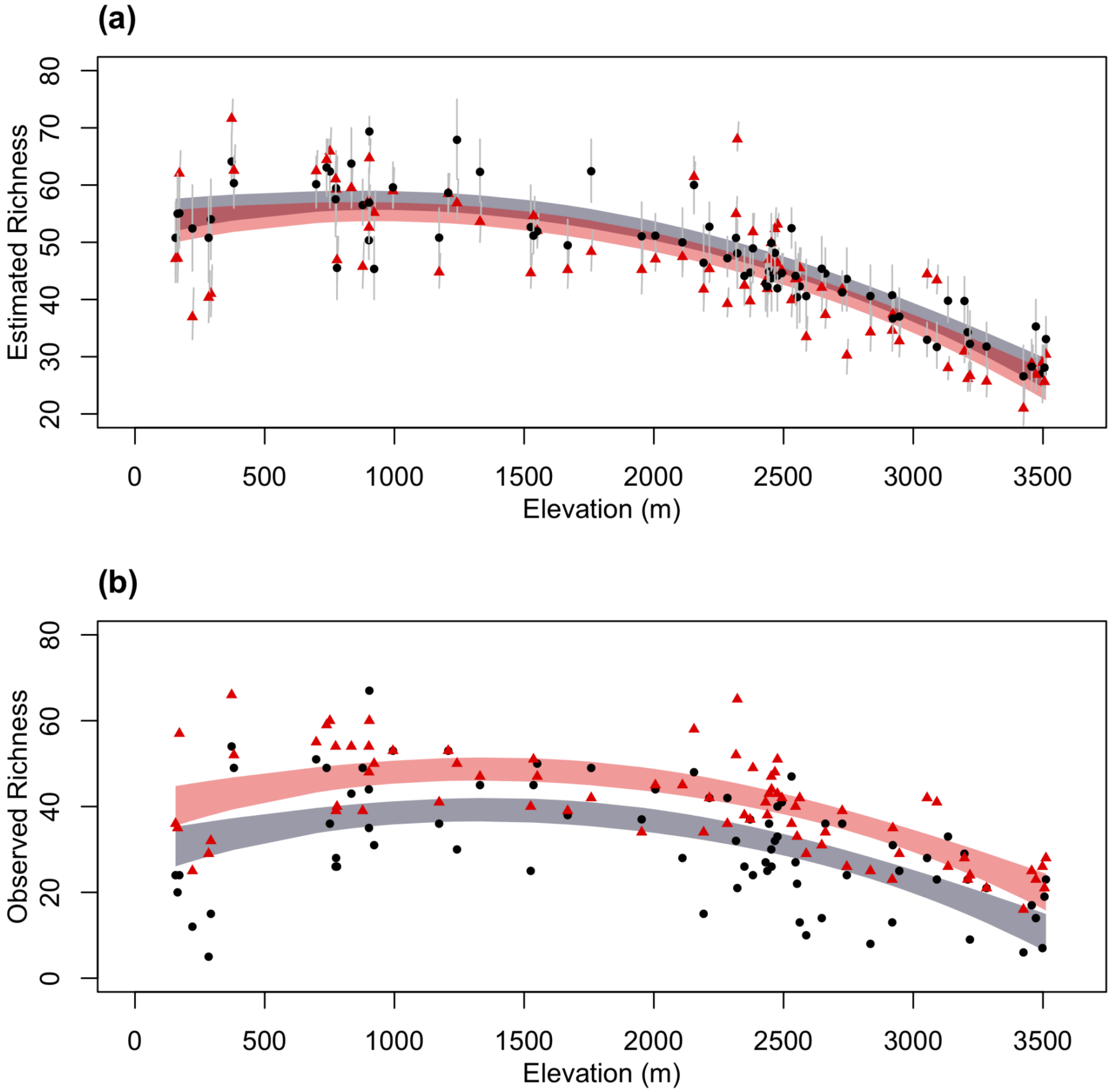


Figure 2. Patterns of species richness after accounting for non-detected species at each site (a) and based on naïve estimates derived solely from detected species (b). Each survey point is represented by its historical richness (black circles) and modern richness (red triangles). For estimated true richness (b), lines through points represent 95% credible intervals of the posterior distribution. Elevational trends for historical (black) and modern (red) 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).

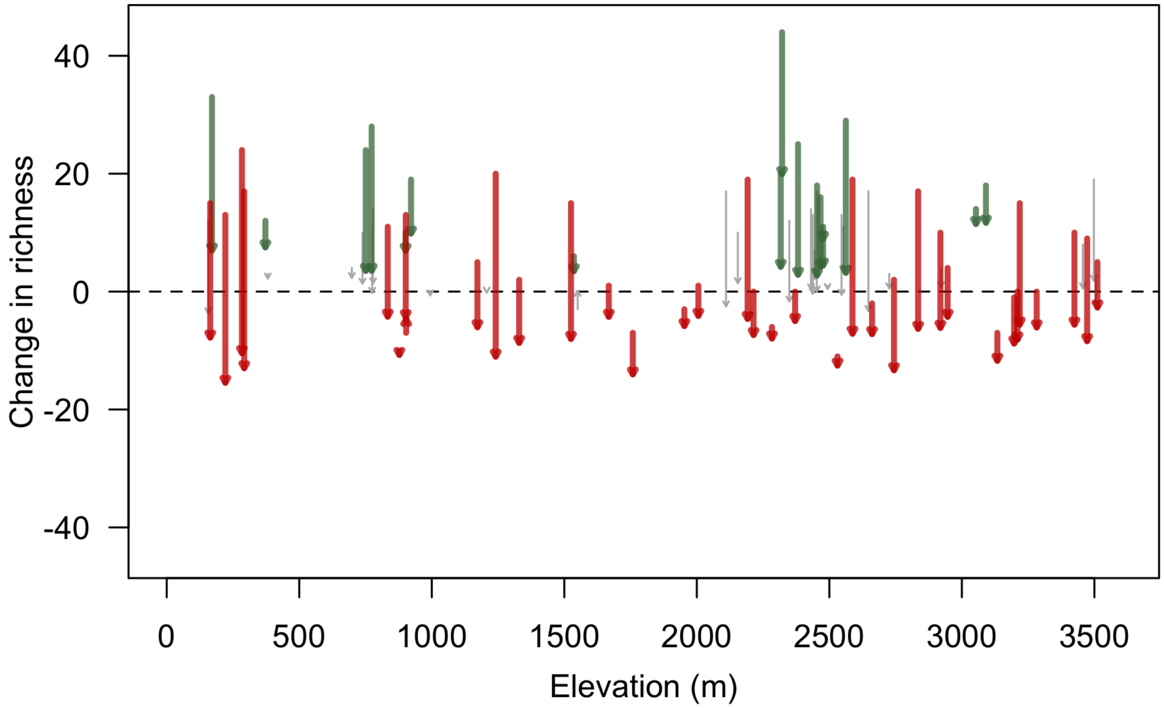


Figure 3. Differences in per-site species richness change over time between observed-only and modeled estimates. The base of each arrow is the difference in species richness at a survey site between historic and modern surveys, as estimated from only those species that were observed. The tip of each arrow is per-site difference in posterior mean richness over time as estimated by modeling the species that were not detected. Red arrows are sites for which estimated true richness (i.e. counting all species) significantly decreased over time (95% credible intervals of richness did not overlap), while green arrows significantly increased in richness over time. Sites for which richness did not significantly change over time are in gray. Note that while richness increased significantly at several sites, all significant estimates of richness change were less after accounting for undetected species.

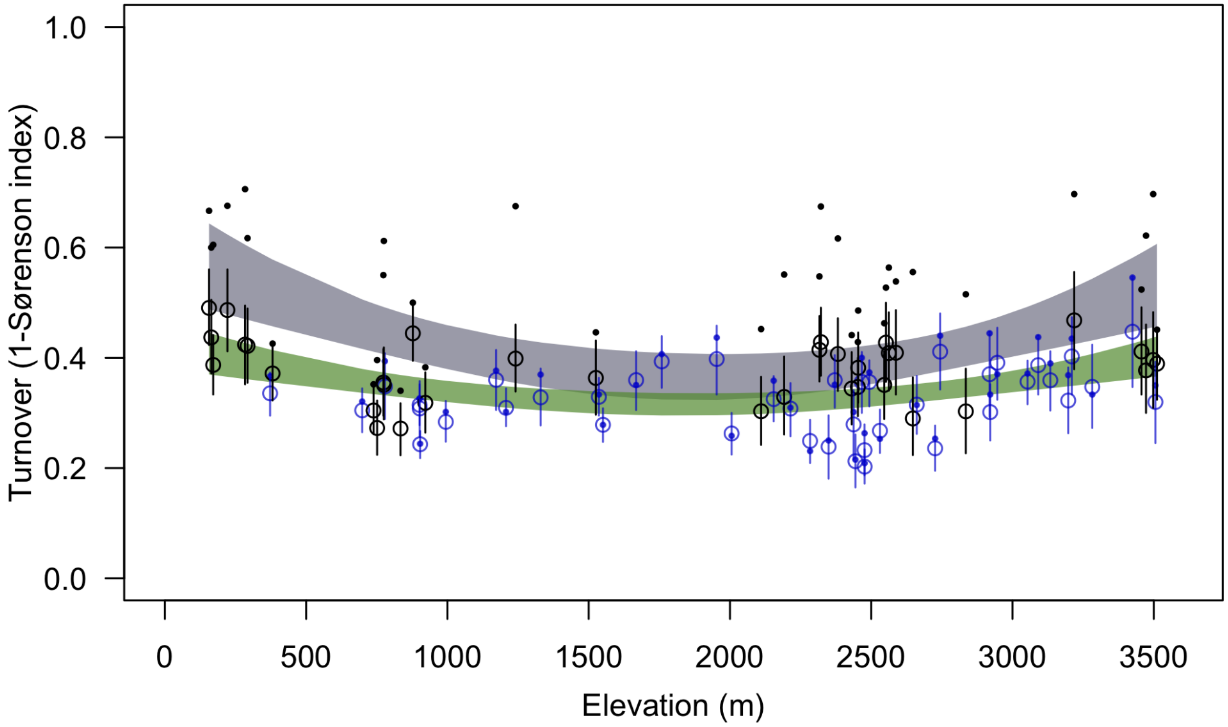


Figure 4. Turnover in historic and modern species communities at each site, as based on observed-only species (small dots) and after accounting for unobserved species (open circles). Turnover estimates that are not significantly different between richness-estimation methods are in blue. Trends lines are 95% confidence intervals of the predicted output from linear regressions of turnover trend with elevation for observed-only species (gray) and including undetected species (green). Both richness methods found quadratic relationships of turnover with elevation, with highest turnover at elevational extremes.

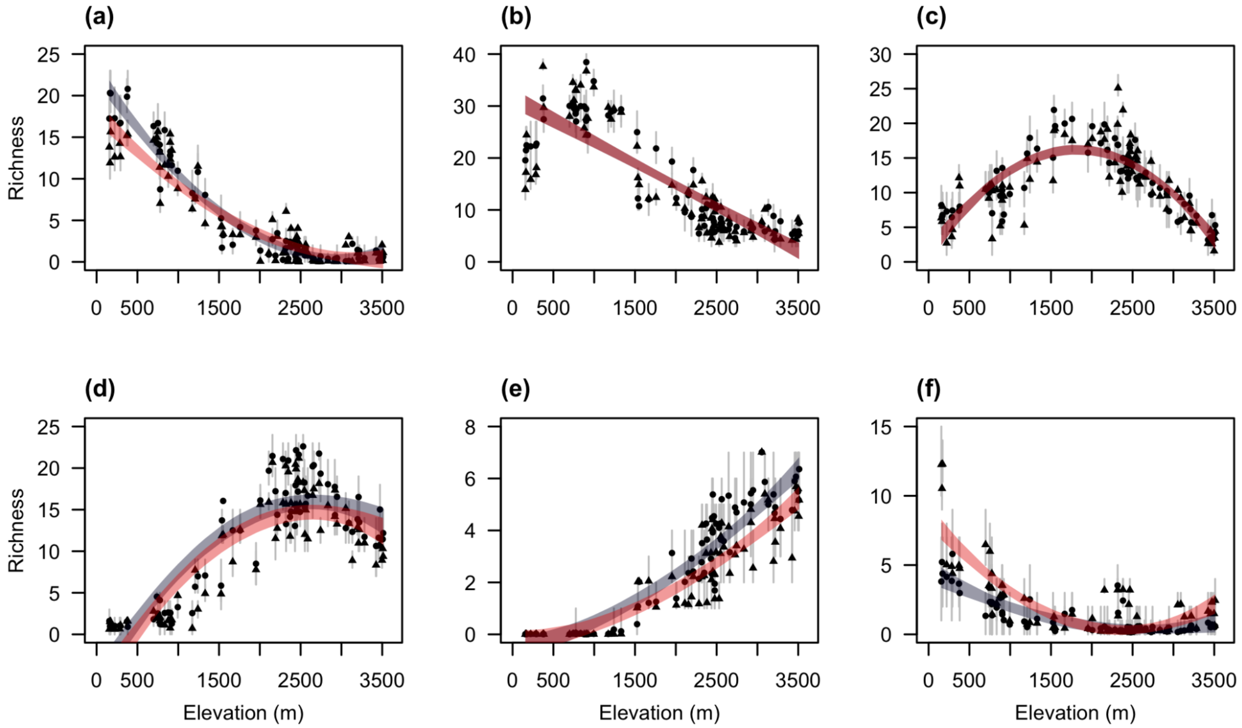


Figure 5. Difference in per-point richness for species of different life zone classes in the historic (circles) and modern (triangles) surveys. All richness estimates include detected and undetected species (uncertainty at points shown by 95% credible intervals lines). Elevational trend lines for each life zone were estimated using general linear models and are depicted as 95% confidence intervals of the trend with elevation for historic richness (gray line) and modern richness (red line). Species life zones consist of: Lower Sonoran species (a); Upper Sonoran species (b); Transition species (c); Canadian species (d); Hudsonian species (e); and unclassified species (f).

Table S1. Species-specific posterior means (± standard deviation) of all parameter values for occupancy (β_0-β_7).

Common Name	**Scientific Name**	**Life Zone**	β_0	β_1	β_2	β_3	β_4	β_5	β_6	β_7
Canada Goose	*Branta canadensis*	Transition	-4.89±1.21	1.15±0.84	-1.44±0.9	-1.24±0.74	-0.69±0.71	0.45±0.59	0.63±0.98	3.33±0.89
Wood Duck	*Aix sponsa*	Lower Sonoran	-4.37±1.2	0.83±0.94	-1.58±0.97	-0.54±0.68	-0.2±0.67	0.22±0.51	-0.44±1.05	1.63±0.92
Gadwall	*Anas strepera*	Unclassified	-8.98±2.66	0.03±1.1	-2.33±1.82	-0.15±0.95	-0.35±0.79	0.36±0.57	-0.59±1.45	-0.28±1.38
Mallard	*Anas platyrhynchos*	Upper Sonoran	-2.59±0.92	1.48±0.77	-0.42±0.62	-0.13±0.54	-0.43±0.61	0.89±0.53	-0.1±0.65	0.3±0.63
Blue-winged Teal	*Anas discors*	Unclassified	-4.47±1.44	-0.28±0.96	1.25±1.21	-0.46±0.84	0.58±0.76	0.29±0.6	-0.06±1.14	0.26±1.12
Cinnamon Teal	*Anas cyanoptera*	Upper Sonoran	-6.27±1.66	0.36±1	-1.5±1.19	0.46±0.74	0.07±0.7	-0.02±0.47	0.07±1.12	0.38±1.13
Green-winged Teal	*Anas crecca*	Unclassified	-6.45±1.87	0.41±1.03	2.52±1.7	-1.11±1.06	0.51±0.8	0.11±0.59	1.54±1.25	-0.47±1.29
Redhead	*Aythya americana*	Unclassified	-5.33±1.59	-0.5±1	-0.92±1.19	-0.47±0.83	-0.44±0.76	0.39±0.57	-0.88±1.34	0.6±1.16
Ring-necked Duck	*Aythya collaris*	Unclassified	-4.94±1.51	0.63±1.01	0.34±1.57	-2.3±1.15	0.15±0.79	-0.25±0.63	-0.73±1.37	1.53±1.19
Bufflehead	*Bucephala albeola*	Canadian	-4.15±1.39	-1.1±0.97	0.34±1.51	-2.4±1.16	-0.11±0.78	-0.23±0.64	-0.68±1.4	1.57±1.21
Common Merganser	*Mergus merganser*	Upper Sonoran	-4.68±1.2	0.58±0.83	-0.32±0.77	-0.45±0.66	-0.33±0.67	0.54±0.54	0.84±0.99	2.26±0.91
Ruddy Duck	*Oxyura jamaicensis*	Unclassified	-5.17±1.64	-0.57±1.04	-0.89±1.22	-0.43±0.86	-0.44±0.78	0.38±0.56	-0.84±1.34	0.63±1.18
Mountain Quail	*Oreortyx pictus*	Canadian	1.4±0.66	-0.5±0.6	-0.6±0.58	-3.85±0.74	-0.61±0.6	-0.23±0.56	2.63±0.72	0.32±0.63
California Quail	*Callipepla californica*	Upper Sonoran	-2.46±0.81	0.19±0.69	-6.45±1.12	-2.82±0.59	-0.22±0.68	0.01±0.42	-0.19±0.66	1.73±0.83
Ring-necked Pheasant	*Phasianus colchicus*	Unclassified	-7.41±2.16	0.22±1.09	-2.62±1.78	-1.19±1.06	-0.41±0.8	0.13±0.59	-0.5±1.43	1.16±1.28
Sooty Grouse	*Dendragapus fuliginosus*	Canadian	-1.54±1	-1.02±0.86	3.71±1.31	-2.28±1.01	-0.03±0.76	-0.31±0.59	1.4±0.88	-0.01±0.89
Wild Turkey	*Meleagris gallopavo*	Unclassified	-5.7±1.57	0.93±1.02	-3.32±1.47	-1.8±0.91	-0.67±0.76	0.11±0.56	0.28±1.18	2.08±1.05
Pied-billed Grebe	*Podilymbus podiceps*	Transition	-5.3±1.52	0.98±0.99	-1.03±1.11	-0.5±0.72	-0.33±0.76	0.35±0.56	1.56±1.05	1.17±1.09
Eared Grebe	*Podiceps nigricollis*	Transition	-3.09±1.38	-0.44±0.91	-0.37±0.98	-0.74±0.79	-0.46±0.75	0.38±0.56	-1.21±1.31	1.35±1.09
Western Grebe	*Aechmophorus occidentalis*	Transition	-4.61±1.4	-0.22±0.96	0.3±1.53	-2.35±1.17	0.05±0.81	-0.25±0.62	-0.7±1.4	1.64±1.19
American White Pelican	*Pelecanus erythrorhynchos*	Transition	-4.56±1.43	-0.25±0.97	0.25±1.5	-2.39±1.19	0.02±0.8	-0.25±0.62	-0.68±1.44	1.63±1.21
Double-crested Cormorant	*Phalacrocorax auritus*	Unclassified	-4.3±1.32	-0.68±0.94	-1.35±0.91	0.13±0.68	0.19±0.69	-0.14±0.53	-0.2±1.12	1.42±1.02
Great Blue Heron	*Ardea herodias*	Upper Sonoran	-4.12±1.01	-0.36±0.76	-1.43±0.62	0.44±0.47	-0.64±0.62	-0.3±0.45	1.2±0.81	2.88±0.85
Great Egret	*Ardea alba*	Unclassified	-8.2±1.97	0.54±1.07	-3.07±1.84	-0.39±0.95	-0.78±0.77	0.49±0.54	0.03±1.14	2.1±1.03
Snowy Egret	*Egretta thula*	Unclassified	-8.67±2.64	-0.05±1.16	-2.55±1.83	0.16±1	-0.46±0.79	0.48±0.58	-0.7±1.42	-0.29±1.36
Cattle Egret	*Bubulcus ibis*	Unclassified	-9.3±2.9	0±1.12	-2.58±1.88	0.38±0.99	-0.48±0.76	0.52±0.55	-0.84±1.42	-0.41±1.33
Green Heron	*Butorides virescens*	Unclassified	-8.25±1.95	-0.13±0.98	-3.91±1.79	0.46±0.89	-0.18±0.73	-0.03±0.5	0.27±1.14	1.78±1.03
Black-crowned Night-Heron	*Nycticorax nycticorax*	Unclassified	-4.72±1.84	-0.87±1.07	-1.5±1.34	0.23±0.84	-0.14±0.75	0.01±0.55	0.12±1.28	0.62±1.19
White-faced Ibis	*Plegadis chihi*	Unclassified	-7.01±2.17	0.29±1.07	-2.77±1.8	-0.5±0.89	-0.5±0.76	0.39±0.55	-1.07±1.3	-0.8±1.26

Turkey Vulture	*Cathartes aura*	Upper Sonoran	-2.95±1	-0.01±0.69	-4.18±0.96	0±0.86	0.34±0.66	-0.1±0.58	-0.38±0.91	3.31±0.98
Osprey	*Pandion haliaetus*	Transition	-2.87±1.13	-0.34±0.79	-1.56±0.82	-1.11±0.67	-0.16±0.65	0.18±0.51	0.27±1.01	3.44±0.97
White-tailed Kite	*Elanus leucurus*	Unclassified	-8.45±2.34	0.01±1.1	-2.58±1.84	-0.58±1	-0.41±0.79	0.26±0.57	1.25±1.32	-0.24±1.38
Bald Eagle	*Haliaeetus leucocephalus*	Transition	-4.6±1.36	1.11±0.93	-0.66±1.05	-1.49±0.91	0±0.75	0.01±0.58	-0.93±1.34	2.35±1.11
Northern Harrier	*Circus cyaneus*	Unclassified	-2.99±1.04	0.07±0.87	-1.47±0.93	-0.95±0.71	0.06±0.69	0.23±0.53	-0.78±0.99	-0.13±0.89
Sharp-shinned Hawk	*Accipiter striatus*	Canadian	-0.15±1.91	-0.45±1.1	-2.28±1.54	-1.02±0.96	-0.4±0.8	0.14±0.6	0.16±1.31	1.36±1.24
Cooper's Hawk	*Accipiter cooperii*	Transition	-1.46±1.39	0.14±0.96	-3.14±1.33	-0.89±1.02	-0.06±0.75	0.07±0.6	-1.34±1.25	1.88±1.18
Northern Goshawk	*Accipiter gentilis*	Canadian	-4.67±1.23	0.53±0.88	2.06±1.3	-0.89±0.85	-0.08±0.73	-0.41±0.58	-0.23±1.1	0.56±1
Red-shouldered Hawk	*Buteo lineatus*	Lower Sonoran	-5.58±1.28	1.29±0.94	-2.91±1.13	-0.2±0.67	-0.42±0.71	-0.12±0.51	0.53±0.93	1.82±0.9
Swainson's Hawk	*Buteo swainsoni*	Upper Sonoran	-4.29±1.17	-1.48±0.97	0.02±0.49	1.48±0.57	-0.18±0.6	-0.54±0.48	-1.11±1	0.23±0.94
Red-tailed Hawk	*Buteo jamaicensis*	Upper Sonoran	1.9±1	-0.39±0.81	-0.51±0.91	0.36±0.78	-0.63±0.7	0.38±0.6	-0.84±0.96	-0.9±0.92
Golden Eagle	*Aquila chrysaetos*	Upper Sonoran	-2.86±1.09	-1.97±0.96	0.51±0.57	0.24±0.6	-0.23±0.71	-0.61±0.58	1.66±0.95	-0.05±1.09
American Kestrel	*Falco sparverius*	Lower Sonoran	-0.88±0.72	-1.6±0.69	-1.52±0.63	1.02±0.6	0.42±0.56	0.04±0.54	-0.77±0.84	0.27±0.72
Peregrine Falcon	*Falco peregrinus*	Unclassified	-6.01±1.97	0.22±1.09	2.07±1.66	-0.85±1.13	0.38±0.82	0.03±0.62	-0.76±1.35	-0.49±1.34
Prairie Falcon	*Falco mexicanus*	Unclassified	-4.63±1.46	0.75±1.05	0.2±0.85	0.26±0.75	0.03±0.7	0.54±0.58	0.41±1.07	-1.06±1.21
Virginia Rail	*Rallus limicola*	Transition	-3.72±1.31	0.92±0.99	-1.65±1.25	-1.7±0.94	-0.32±0.77	0.02±0.58	-0.3±1.1	-1.13±1.16
Sora	*Porzana carolina*	Unclassified	-4.19±1.3	1.11±0.93	0.77±1.41	-2.48±1.1	0.28±0.79	-0.25±0.62	-1.18±1.25	1±1.01
Common Moorhen	*Gallinula chloropus*	Unclassified	-7.26±2.1	0.27±1.07	-2.86±1.75	-0.67±1.04	-0.53±0.79	0.27±0.57	0.69±1.29	0.88±1.27
American Coot	*Fulica americana*	Unclassified	-3.89±1.14	0.47±0.85	0.2±0.71	-0.07±0.61	-0.18±0.64	0.7±0.53	-1.78±1.14	0.4±0.87
Sandhill Crane	*Grus canadensis*	Unclassified	-4.34±1.36	0.98±0.95	-0.04±1.37	-2.75±1.15	0.18±0.8	-0.32±0.62	-0.9±1.34	2.05±1.12
Killdeer	*Charadrius vociferus*	Upper Sonoran	-2.29±0.73	-1.56±0.62	-1.89±0.54	0.76±0.55	0.31±0.56	0.1±0.5	0.57±0.7	2.38±0.72
Black-necked Stilt	*Himantopus mexicanus*	Unclassified	-9.51±2.64	-0.24±1.12	-3.28±1.91	0.47±0.92	-0.11±0.75	0.13±0.48	-0.95±1.34	-0.41±1.35
American Avocet	*Recurvirostra americana*	Unclassified	-8.93±2.64	0±1.13	-2.48±1.92	-0.25±0.96	-0.38±0.76	0.36±0.57	-0.51±1.44	-0.3±1.37
Spotted Sandpiper	*Actitis macularius*	Hudsonian	-2.82±0.86	-0.9±0.61	2.02±0.65	-0.27±0.56	-0.37±0.62	0.03±0.52	2.37±0.76	2.46±0.75
Long-billed Curlew	*Numenius americanus*	Unclassified	-8.75±2.59	0.01±1.13	-2.3±1.84	-0.2±1	-0.38±0.8	0.36±0.55	-0.58±1.43	-0.27±1.39
Wilson's Snipe	*Gallinago delicata*	Transition	-2.98±1.09	0.45±0.82	-2.21±1.03	-2.18±0.91	0.46±0.72	-0.49±0.58	-1.44±1.21	1.81±0.91
Wilson's Phalarope	*Phalaropus tricolor*	Transition	-5.5±1.82	0.46±1.07	-1.04±1.29	-0.42±0.86	-0.21±0.77	0.33±0.57	-0.86±1.37	0.63±1.19
California Gull	*Larus californicus*	Transition	-5.48±1.67	-0.21±1.04	3.19±1.63	-0.62±1.08	0.19±0.79	-0.04±0.6	1.87±1.24	-0.58±1.33
Black Tern	*Chlidonias niger*	Transition	-8.79±2.54	-0.33±1.1	-3.12±1.91	0.55±0.95	0.03±0.78	-0.08±0.5	-0.77±1.38	-0.32±1.35
Forster's Tern	*Sterna forsteri*	Transition	-4.08±1.52	-0.31±0.97	0.28±1.59	-2.32±1.16	0.03±0.82	-0.25±0.62	-0.74±1.4	1.61±1.19
Rock Pigeon	*Columba livia*	Unclassified	-4.78±1.5	0.15±0.99	-3.55±1.58	-1.2±0.82	-0.5±0.74	0.27±0.51	-1.83±1.13	-0.85±0.95
Band-tailed Pigeon	*Patagioenas fasciata*	Transition	-2.64±0.86	1.25±0.68	-0.88±0.74	-1.98±0.7	0.51±0.68	0.1±0.54	2.06±0.78	0.44±0.81
Eurasian Collared-Dove	*Streptopelia decaocto*	Unclassified	-5.33±1.69	0.59±1.04	-3.43±1.67	-1.69±0.95	-0.65±0.78	0.11±0.54	-1.19±1.26	-0.02±1.05

Mourning Dove	*Zenaida macroura*	Upper Sonoran	-0.82±0.75	1.53±0.65	-4.25±0.83	0.24±0.69	0.49±0.68	0±0.57	-2.52±0.86	0.73±0.68
Common Ground-Dove	*Columbina passerina*	Unclassified	-8.22±2.65	-0.03±1.12	-2.59±1.9	-0.27±1.04	-0.38±0.8	0.33±0.58	-0.52±1.43	-0.28±1.36
Rose-ringed Parakeet	*Psittacula krameri*	Unclassified	-8.72±2.66	-0.01±1.12	-2.36±1.85	-0.25±0.98	-0.37±0.79	0.36±0.56	-0.59±1.43	-0.28±1.36
Yellow-billed Cuckoo	*Coccyzus americanus*	Unclassified	-5.27±2.13	-0.71±1.11	-3.13±1.83	-1.33±1.12	0.22±0.8	-0.36±0.63	-0.76±1.42	-0.43±1.36
Greater Roadrunner	*Geococcyx californianus*	Lower Sonoran	-4.98±1.85	-0.41±0.99	-5.01±1.84	-1.28±1.24	0.04±0.77	-0.32±0.61	1.67±1.2	-0.8±1.33
Barn Owl	*Tyto alba*	Lower Sonoran	-7.72±2.36	-0.62±1.13	-3.05±1.93	-0.21±1.12	0.26±0.78	-0.42±0.59	0.95±1.34	-0.27±1.42
Western Screech-Owl	*Megascops kennicottii*	Upper Sonoran	-6.72±2.16	-0.65±1.12	-3.13±1.83	-1.02±1.14	0.24±0.79	-0.37±0.6	-0.56±1.43	1.17±1.29
Great Horned Owl	*Bubo virginianus*	Upper Sonoran	-1.97±1.22	-0.62±0.93	-3.02±1.2	-1.11±0.81	-0.28±0.73	0±0.56	-1.39±1.12	-0.47±1
Northern Pygmy-Owl	*Glaucidium gnoma*	Transition	-4.56±1.54	0.7±1.02	-1.96±1.53	-1.64±0.97	-0.36±0.78	0±0.61	0.27±1.22	-0.73±1.26
Burrowing Owl	*Athene cunicularia*	Lower Sonoran	-8.65±2.44	-0.81±1.12	-3.48±1.78	0.58±0.88	0.46±0.77	-0.65±0.55	0.27±1.24	-0.46±1.34
Spotted Owl	*Strix occidentalis*	Transition	-5.11±1.78	-0.77±1.05	0.85±1.8	-1.86±1.21	-0.08±0.82	-0.21±0.63	-0.56±1.48	1.13±1.34
Great Gray Owl	*Strix nebulosa*	Canadian	-5.33±1.67	-0.7±1.07	0.27±1.74	-2.09±1.2	-0.03±0.8	-0.21±0.62	1.14±1.34	-0.32±1.36
Lesser Nighthawk	*Chordeiles acutipennis*	Lower Sonoran	-8.19±2.42	-0.76±1.12	-3.15±1.85	0.28±0.91	0.38±0.79	-0.56±0.56	0.58±1.2	-0.37±1.33
Common Nighthawk	*Chordeiles minor*	Canadian	0.53±0.82	-1.21±0.74	-0.26±0.59	-0.97±0.58	-0.71±0.62	-0.46±0.52	-2.16±0.91	1.11±0.69
Common Poorwill	*Phalaenoptilus nuttallii*	Upper Sonoran	-3.33±1.37	-0.42±0.98	-2.16±1.16	-0.38±0.81	0.73±0.77	-0.56±0.57	0.18±1.07	-1.03±1.24
Black Swift	*Cypseloides niger*	Transition	-4.59±1.55	0.63±1.02	0.41±1.54	-2.36±1.16	0.15±0.8	-0.25±0.63	1.59±1.26	-0.6±1.32
Vaux's Swift	*Chaetura vauxi*	Unclassified	-3.3±1.33	-0.03±0.95	-0.92±1.05	-0.44±0.79	0.37±0.75	-0.54±0.6	-1.17±1.33	1.49±1.12
White-throated Swift	*Aeronautes saxatalis*	Transition	0.42±0.83	0.07±0.69	-2.28±0.77	-2.55±0.71	0.28±0.64	-0.24±0.53	1.07±0.72	-2.37±0.84
Black-chinned Hummingbird	*Archilochus alexandri*	Upper Sonoran	-3.62±1.25	-0.55±0.95	-2.9±1.1	-0.23±0.65	-0.22±0.7	-0.02±0.5	-1.51±1.03	-0.21±0.87
Anna's Hummingbird	*Calypte anna*	Upper Sonoran	-1.02±0.96	2.25±0.8	-3.79±0.98	-2.64±0.7	-0.62±0.7	0.22±0.47	-0.71±0.74	-1.05±0.73
Calliope Hummingbird	*Stellula calliope*	Canadian	0.58±0.91	0.32±0.9	1.61±0.99	-2.95±0.82	0.98±0.77	0.09±0.6	1.43±0.98	0.03±0.87
Belted Kingfisher	*Megaceryle alcyon*	Upper Sonoran	-1.97±0.84	-0.71±0.68	-1.36±0.51	-0.52±0.45	0.34±0.55	0.19±0.45	1.49±0.71	1.24±0.7
Lewis's Woodpecker	*Melanerpes lewis*	Transition	-0.33±1.32	-1.13±0.99	-2.1±1.19	-1.15±0.84	0.4±0.77	-0.58±0.61	-0.59±1.2	1.45±1.01
Acorn Woodpecker	*Melanerpes formicivorus*	Upper Sonoran	-3.88±0.85	0.05±0.74	-6.35±1.14	-2.89±0.65	-0.46±0.69	-0.19±0.46	2.38±0.71	2.39±0.74
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Hudsonian	-1.48±0.77	0.49±0.68	4.61±1.35	-2.1±0.9	0.11±0.74	-0.44±0.56	-0.04±0.69	-1.76±0.72
Red-breasted Sapsucker	*Sphyrapicus ruber*	Transition	1.85±0.87	-0.37±0.73	1.12±0.71	-3.14±0.71	0.62±0.69	-0.23±0.56	-0.49±0.68	-0.03±0.73
Nuttall's Woodpecker	*Picoides nuttallii*	Upper Sonoran	-4.31±1.13	0.47±0.81	-7.17±1.48	-2.11±0.76	-0.22±0.7	-0.67±0.52	-0.19±0.72	1.23±0.85
Downy Woodpecker	*Picoides pubescens*	Transition	-1.59±0.86	0.25±0.74	-4.09±0.95	-2.1±0.71	-0.09±0.69	0.14±0.5	0.05±0.74	1.21±0.76
Hairy Woodpecker	*Picoides villosus*	Canadian	5.04±1.18	-0.85±0.87	1.17±0.52	-2.35±0.62	0±0.55	-0.84±0.53	1.58±0.92	-1.85±0.81
White-headed Woodpecker	*Picoides albolarvatus*	Transition	1.46±0.73	0.38±0.64	2.07±0.77	-4.51±0.87	-0.17±0.69	-0.58±0.61	0.34±0.7	0±0.72

Black-backed Woodpecker	*Picoides arcticus*	Hudsonian	-2.64±1.25	-0.77±0.86	3.99±1.46	-1.78±1.09	-0.07±0.77	-0.35±0.61	1.83±1.06	1.49±1.02
Northern Flicker	*Colaptes auratus*	Upper Sonoran	5.25±1.06	-0.84±0.82	-0.55±0.49	-1.74±0.49	-0.55±0.53	-0.35±0.43	1.74±0.81	-1.57±0.73
Pileated Woodpecker	*Dryocopus pileatus*	Transition	-1.74±0.88	0.15±0.63	0.62±0.8	-3.72±0.94	-0.06±0.69	-0.42±0.62	2.57±0.8	2.3±0.79
Olive-sided Flycatcher	*Contopus cooperi*	Canadian	0.87±0.7	0.79±0.64	1.37±0.55	-2.5±0.59	0.12±0.56	0.17±0.52	0.77±0.64	0.47±0.68
Western Wood-Pewee	*Contopus sordidulus*	Transition	4.27±0.94	0.38±0.8	-0.24±0.37	-1.73±0.44	-0.91±0.45	-0.14±0.4	0.36±0.72	-0.52±0.73
Willow Flycatcher	*Empidonax traillii*	Transition	-2.69±0.94	0.04±0.77	-2.81±0.93	-0.83±0.61	0.29±0.67	-0.42±0.5	0.14±0.82	1.28±0.82
Hammond's Flycatcher	*Empidonax hammondii*	Canadian	-2.38±0.85	-0.16±0.6	2.02±0.86	-2.89±0.82	-0.57±0.69	-0.68±0.61	2.48±0.79	2.4±0.79
Gray Flycatcher	*Empidonax wrightii*	Transition	-2.72±0.92	0.48±0.77	2.04±1.23	-1.91±0.85	0.23±0.76	-0.18±0.59	-2.01±1.08	0.03±0.73
Dusky Flycatcher	*Empidonax oberholseri*	Canadian	0.02±0.75	0.02±0.67	2.93±0.94	-1.25±0.72	0.67±0.73	0.18±0.57	0.9±0.84	-0.11±0.68
Pacific-slope Flycatcher	*Empidonax difficilis*	Transition	-3.8±1.1	0.2±0.77	-3.75±1.02	-2.48±0.79	-0.24±0.72	0.03±0.54	4.18±0.97	-0.13±1.05
Black Phoebe	*Sayornis nigricans*	Lower Sonoran	-0.35±0.65	-0.72±0.65	-2.72±0.73	0.77±0.66	0.37±0.66	0.57±0.57	-0.47±0.67	-1.67±0.81
Say's Phoebe	*Sayornis saya*	Unclassified	-5.08±1.83	0.2±1.04	-4.04±1.77	-0.37±0.98	-0.34±0.75	0.1±0.6	-1.76±1.38	-1.55±1.27
Ash-throated Flycatcher	*Myiarchus cinerascens*	Upper Sonoran	-1.06±0.82	-0.99±0.75	-6.39±1.18	-2.13±0.82	-0.32±0.73	-0.47±0.54	-0.97±0.78	0.24±0.81
Western Kingbird	*Tyrannus verticalis*	Lower Sonoran	-5.81±1.67	-0.3±0.91	-7.3±1.97	1.01±1.18	-0.27±0.76	0.11±0.61	-0.21±1.06	-0.29±1.07
Loggerhead Shrike	*Lanius ludovicianus*	Lower Sonoran	-3.51±1.16	-1.46±0.99	-1.21±0.82	0.9±0.66	0.23±0.7	-0.62±0.52	-0.43±0.98	-0.75±1
Bell's Vireo	*Vireo bellii*	Lower Sonoran	-6.94±1.65	-1.43±1.03	-4.82±1.67	-0.25±0.89	0.83±0.79	-0.83±0.57	1.58±1.03	1.63±1.01
Cassin's Vireo	*Vireo cassinii*	Transition	1.34±0.68	-0.04±0.62	-0.38±0.36	-1.66±0.42	0.05±0.48	-1.01±0.51	1.1±0.59	0.1±0.56
Hutton's Vireo	*Vireo huttoni*	Upper Sonoran	-6.32±1.46	1.42±0.94	-3.46±1.42	-2.18±0.87	-0.88±0.78	0.08±0.56	3.23±1.05	-0.77±1.26
Warbling Vireo	*Vireo gilvus*	Transition	1.55±0.6	-0.06±0.58	-1.5±0.4	-1.17±0.38	0.92±0.44	-0.01±0.39	1.16±0.55	0.16±0.5
Gray Jay	*Perisoreus canadensis*	Unclassified	-5.33±1.78	0.47±1.07	1.68±1.58	-1.1±1.04	0.37±0.8	0.05±0.61	-0.79±1.38	1.6±1.23
Steller's Jay	*Cyanocitta stelleri*	Transition	3.69±1.04	0.42±0.8	2.26±0.57	-3.53±0.69	0.08±0.55	-0.38±0.5	1.35±0.77	0.39±0.83
Western Scrub-Jay	*Aphelocoma californica*	Upper Sonoran	-0.78±0.65	-0.67±0.65	-4.46±0.84	-2.21±0.55	-0.75±0.68	0.25±0.46	-0.25±0.63	0.28±0.66
Pinyon Jay	*Gymnorhinus cyanocephalus*	Transition	-3.42±1.31	0.75±0.98	0.07±1.49	-2.27±1.13	0.12±0.83	-0.22±0.61	-1.27±1.3	-1.05±1.23
Yellow-billed Magpie	*Pica nuttalli*	Lower Sonoran	-6.69±1.93	-0.22±1.04	-3.09±1.59	-0.97±0.92	-0.11±0.76	-0.1±0.55	-0.68±1.41	1.78±1.21
Clark's Nutcracker	*Nucifraga columbiana*	Hudsonian	0.17±0.73	-0.74±0.62	5.33±1.12	0.06±0.81	-0.12±0.76	-0.1±0.58	-2.77±0.78	-1.93±0.72
American Crow	*Corvus brachyrhynchos*	Lower Sonoran	-6.32±1.46	-0.79±0.92	-4.88±1.71	-0.69±0.81	-0.17±0.71	0.4±0.49	0.3±0.85	1.45±0.78
Common Raven	*Corvus corax*	Upper Sonoran	-0.64±0.6	3.42±0.62	-0.2±0.37	-0.36±0.35	-0.06±0.41	-0.42±0.38	-1.12±0.58	-0.79±0.58
Horned Lark	*Eremophila alpestris*	Lower Sonoran	-3.54±1.03	-0.64±0.86	-1.46±0.68	0.75±0.54	1.03±0.65	0±0.46	-1.38±0.98	0.23±0.82
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Upper Sonoran	-5.06±1.36	1.06±0.94	-2.73±1.15	-0.17±0.71	-0.51±0.71	0.16±0.51	-0.44±1.05	1.96±1.01
Tree Swallow	*Tachycineta bicolor*	Lower	-3.19±0.81	0.82±0.68	-1.88±0.82	-0.31±0.52	-0.49±0.6	-0.09±0.44	-0.77±0.75	3.28±0.85

		Sonoran								
Violet-green Swallow	*Tachycineta thalassina*	Transition	-0.93±0.68	-0.3±0.6	-1.64±0.54	-1.17±0.46	-0.4±0.54	0.08±0.43	1.42±0.6	1.03±0.6
Barn Swallow	*Hirundo rustica*	Lower Sonoran	-5.05±1.19	0.66±0.89	-2.05±0.87	0.38±0.53	0.19±0.66	-0.08±0.45	1.48±0.87	0.33±0.83
Cliff Swallow	*Petrochelidon pyrrhonota*	Upper Sonoran	-3.33±0.99	-0.91±0.83	-3.73±0.98	0.74±0.75	0.72±0.72	-0.15±0.53	-0.62±0.87	1.3±0.9
Mountain Chickadee	*Poecile gambeli*	Hudsonian	3.85±1.29	0.57±0.89	5.64±1.33	-2.26±1.03	0.26±0.76	-0.19±0.6	1.25±1.08	-0.21±1.1
Chestnut-backed Chickadee	*Poecile rufescens*	Unclassified	-4.27±1.63	0.72±1.04	-1.57±1.45	-2.42±1.16	-0.21±0.79	-0.24±0.62	1.56±1.28	-0.51±1.31
Oak Titmouse	*Baeolophus inornatus*	Upper Sonoran	-3.35±0.96	-0.06±0.8	-8.5±1.35	-3.74±0.65	-0.46±0.71	-0.28±0.43	-0.22±0.68	0.75±0.79
Bushtit	*Psaltriparus minimus*	Upper Sonoran	-1.64±0.64	0.16±0.61	-3.78±0.75	-1.48±0.55	0.26±0.64	0.02±0.45	0.46±0.6	1.1±0.63
Red-breasted Nuthatch	*Sitta canadensis*	Canadian	1.48±0.82	0.75±0.7	2.09±0.58	-2.11±0.57	0±0.57	-0.19±0.49	0.49±0.66	0.2±0.75
White-breasted Nuthatch	*Sitta carolinensis*	Upper Sonoran	1.23±0.55	0.32±0.52	-0.24±0.34	-0.36±0.32	0.12±0.39	-0.1±0.36	-0.59±0.47	-0.45±0.5
Pygmy Nuthatch	*Sitta pygmaea*	Transition	-0.01±0.61	-0.35±0.62	2.19±0.79	-1.32±0.57	-0.2±0.66	-0.42±0.51	-3.07±0.76	-1.39±0.6
Brown Creeper	*Certhia americana*	Transition	2.66±0.87	0.64±0.69	2.18±0.59	-2.99±0.63	0.44±0.56	-0.01±0.49	0.64±0.74	-1.17±0.76
Rock Wren	*Salpinctes obsoletus*	Upper Sonoran	-0.03±0.77	-1.91±0.69	0.93±0.51	0.55±0.51	-0.22±0.52	0.11±0.48	-0.15±0.61	0.4±0.59
Canyon Wren	*Catherpes mexicanus*	Upper Sonoran	-1.29±0.79	-0.46±0.69	-3.46±0.86	-2.06±0.63	0.2±0.65	0.03±0.49	1.53±0.74	-1.1±0.8
Bewick's Wren	*Thryomanes bewickii*	Upper Sonoran	-1.77±0.89	-0.1±0.75	-2.77±0.75	1.74±0.78	-1.28±0.74	-0.05±0.58	-1.63±0.96	-1.12±0.94
House Wren	*Troglodytes aedon*	Upper Sonoran	0.58±0.6	0.49±0.57	-0.5±0.42	-0.23±0.41	-0.21±0.46	0.08±0.41	-0.89±0.53	-0.65±0.53
Winter Wren	*Troglodytes hiemalis*	Transition	-3.97±1.08	1.01±0.78	0.54±0.94	-1.98±0.83	0.39±0.74	0.02±0.58	2.22±0.92	0.44±0.97
Marsh Wren	*Cistothorus palustris*	Upper Sonoran	-7.89±2.22	0.29±1.06	-3.05±1.9	-0.89±0.96	-0.55±0.76	0.29±0.55	0.88±1.25	0.93±1.22
Blue-gray Gnatcatcher	*Polioptila caerulea*	Upper Sonoran	-0.78±0.73	-1.19±0.72	-3.99±0.89	-1.97±0.62	0.55±0.66	-0.36±0.5	-0.36±0.69	-0.8±0.68
American Dipper	*Cinclus mexicanus*	Canadian	-1.86±0.82	-1.22±0.7	1.57±0.58	-0.08±0.46	-0.16±0.61	-0.28±0.48	0.02±0.71	0.74±0.72
Golden-crowned Kinglet	*Regulus satrapa*	Canadian	-0.5±0.78	0.42±0.66	1.71±0.71	-3.24±0.72	-0.01±0.65	-0.57±0.56	2.45±0.69	1.51±0.67
Ruby-crowned Kinglet	*Regulus calendula*	Canadian	1.21±0.69	-3.42±0.69	1.77±0.54	-0.35±0.48	0.24±0.67	-0.19±0.52	-0.02±0.63	-0.44±0.65
Western Bluebird	*Sialia mexicana*	Upper Sonoran	0.13±0.59	0.11±0.55	-3.26±0.68	-1.43±0.62	0.41±0.6	-0.35±0.52	-1.33±0.63	-0.16±0.56
Mountain Bluebird	*Sialia currucoides*	Hudsonian	-1.05±0.66	-1.02±0.64	3.46±1.02	-0.46±0.71	0.03±0.72	-0.06±0.54	-1.61±0.68	-1.07±0.63
Townsend's Solitaire	*Myadestes townsendi*	Canadian	-1.96±0.7	0.91±0.65	4.91±1.08	-3.73±0.76	0.6±0.69	-0.37±0.52	1.74±0.61	2.27±0.7
Swainson's Thrush	*Catharus ustulatus*	Transition	-1.44±0.9	-2.64±0.88	-1.73±0.72	-0.84±0.66	0.33±0.73	-0.62±0.58	1.21±0.88	1.18±0.91
Hermit Thrush	*Catharus guttatus*	Canadian	-1.01±0.62	-0.65±0.57	3.05±0.7	-0.65±0.57	0.04±0.65	-0.56±0.51	2.16±0.69	-0.01±0.57
American Robin	*Turdus migratorius*	Transition	2.83±0.84	0.93±0.83	1.97±1.39	-1.26±0.92	-0.25±0.67	1.23±0.55	0.87±0.84	0.96±0.88
Wrentit	*Chamaea fasciata*	Upper Sonoran	-1.85±0.87	-0.43±0.72	-5.98±1.27	-3.88±0.79	-0.38±0.68	-0.1±0.52	0.07±0.68	-0.42±0.68
Northern Mockingbird	*Mimus polyglottos*	Lower Sonoran	-4.36±1.21	1.02±0.93	-3.07±1.21	0.06±0.64	-0.1±0.7	-0.45±0.47	-0.55±0.81	-0.04±0.75

Sage Thrasher	*Oreoscoptes montanus*	Transition	-7.75±2.4	-0.58±1.11	-2.87±1.84	-0.13±0.98	0.26±0.78	-0.43±0.56	-0.6±1.44	-0.32±1.37
California Thrasher	*Toxostoma redivivum*	Upper Sonoran	-3.77±1.11	-0.46±0.82	-4.82±1.41	-2.05±0.72	-0.03±0.71	-0.09±0.47	0.96±0.74	-0.56±0.82
Le Conte's Thrasher	*Toxostoma lecontei*	Unclassified	-7.56±2.37	-0.6±1.12	-2.93±1.72	-0.21±0.96	0.28±0.8	-0.43±0.56	-0.66±1.4	-0.35±1.36
European Starling	*Sturnus vulgaris*	Upper Sonoran	-4.72±1.23	2.07±0.98	-2.97±1.13	-1.33±0.76	-1.25±0.77	0.75±0.57	-0.83±0.9	1.24±0.86
American Pipit	*Anthus rubescens*	Unclassified	-6.8±1.56	-0.27±0.96	0.99±0.85	0.67±0.7	1.03±0.71	0.56±0.54	1.45±1.01	1.29±1.07
Phainopepla	*Phainopepla nitens*	Upper Sonoran	-4.6±1.34	0.19±0.89	-5.95±1.72	-2.14±0.89	-0.35±0.74	-0.29±0.53	0.09±0.8	-0.42±0.8
Orange-crowned Warbler	*Vermivora celata*	Upper Sonoran	0.37±0.89	-0.79±0.85	-0.1±0.51	-0.87±0.46	0.13±0.55	0.07±0.43	1.67±0.88	-0.29±0.63
Nashville Warbler	*Vermivora ruficapilla*	Transition	0.16±0.76	-0.37±0.68	0.62±0.6	-2.6±0.61	0.27±0.61	-0.09±0.52	2.84±0.78	1.18±0.65
Yellow Warbler	*Dendroica petechia*	Transition	-0.08±0.62	-0.81±0.56	-3.97±0.72	-1.19±0.62	0.81±0.67	-0.18±0.53	0.84±0.62	1.96±0.64
Yellow-rumped Warbler (Audubon race)	*Dendroica coronata*	Canadian	2.08±0.97	-0.09±0.82	4.59±1.02	-1.36±0.84	0.4±0.72	-0.18±0.57	2.09±0.94	2.53±1.05
Black-throated Gray Warbler	*Dendroica nigrescens*	Transition	0.5±0.63	-0.96±0.57	-1.85±0.67	-3.2±0.73	-0.83±0.63	-0.42±0.57	0.87±0.64	-0.22±0.65
Townsend's Warbler	*Dendroica townsendi*	Unclassified	-6.62±2.09	-0.15±1.04	-3.77±1.8	-0.77±1.01	-0.22±0.77	0.01±0.58	2.24±1.26	-0.49±1.36
Hermit Warbler	*Dendroica occidentalis*	Canadian	-0.46±0.63	0.18±0.56	0.89±0.55	-2.22±0.57	-0.31±0.6	-0.61±0.54	2.13±0.64	0.91±0.6
MacGillivray's Warbler	*Oporornis tolmiei*	Transition	1.37±0.93	-0.21±0.73	0.34±0.53	-2.56±0.6	-0.02±0.58	-0.65±0.56	1.17±0.66	0.79±0.67
Common Yellowthroat	*Geothlypis trichas*	Lower Sonoran	-4.41±1.22	0.13±0.87	-5.04±1.52	-0.81±0.78	0.26±0.72	-0.85±0.5	-0.97±0.82	0.29±0.77
Wilson's Warbler	*Wilsonia pusilla*	Canadian	-0.39±0.67	-0.08±0.61	0.39±0.43	0.12±0.4	-1.18±0.49	-0.45±0.42	1.44±0.55	0.95±0.53
Yellow-breasted Chat	*Icteria virens*	Lower Sonoran	-5.04±1.09	-1.23±0.84	-5.15±1.32	-1.33±0.74	0.08±0.7	-0.14±0.49	1.97±0.8	2.29±0.81
Green-tailed Towhee	*Pipilo chlorurus*	Canadian	1.38±0.77	-1.18±0.69	3.13±0.94	-2.75±0.77	-0.34±0.7	-0.71±0.58	-0.47±0.65	-0.75±0.64
Spotted Towhee	*Pipilo maculatus*	Upper Sonoran	0.27±0.71	0.91±0.65	-5.43±0.89	-3.09±0.63	0.19±0.64	-0.25±0.47	0.96±0.7	-0.47±0.68
California Towhee	*Pipilo crissalis*	Upper Sonoran	-2.51±0.9	-0.56±0.75	-6.98±1.27	-2.92±0.66	-0.27±0.71	-0.14±0.45	-0.31±0.67	0.71±0.77
Rufous-crowned Sparrow	*Aimophila ruficeps*	Upper Sonoran	-5.75±1.58	0.35±0.97	-4.57±1.73	-1.82±0.83	-0.55±0.74	0.06±0.51	0.98±0.92	-0.29±1.02
Chipping Sparrow	*Spizella passerina*	Upper Sonoran	2.35±0.75	-1.14±0.71	1.09±1.01	-0.04±0.62	0.87±0.65	-0.34±0.45	0.76±0.74	0.04±0.64
Brewer's Sparrow	*Spizella breweri*	Transition	-2.24±1.17	-0.19±0.94	-2.96±1.22	-1±0.73	0.3±0.73	-0.66±0.58	-1.24±1.03	-1.68±1.13
Vesper Sparrow	*Pooecetes gramineus*	Transition	-2.73±1.06	0.03±0.87	2.51±1.49	-1.67±0.92	0.15±0.75	-0.19±0.57	-2.05±1.11	-1.82±1.07
Lark Sparrow	*Chondestes grammacus*	Upper Sonoran	-1.52±0.77	0.22±0.67	-3.92±0.84	-0.6±0.62	0.56±0.65	-0.61±0.51	-1.32±0.73	-0.08±0.71
Black-throated Sparrow	*Amphispiza bilineata*	Upper Sonoran	-5.66±1.98	-0.64±1.08	-2.78±1.76	-1.27±1.05	0.17±0.8	-0.34±0.61	-0.77±1.42	-0.45±1.34
Sage Sparrow	*Amphispiza belli*	Upper Sonoran	-1.18±0.82	-0.4±0.77	-2.22±0.9	-1.34±0.63	0.11±0.69	-0.57±0.53	-0.69±0.78	-2.06±1.04
Savannah Sparrow	*Passerculus sandwichensis*	Transition	-1.55±0.74	0.63±0.72	-1.25±0.59	0.1±0.42	1.18±0.6	-0.33±0.42	-3.11±0.94	-1.27±0.62
Grasshopper Sparrow	*Ammodramus savannarum*	Transition	-8.55±2.68	-0.62±1.13	-3.09±2.01	0.17±1.06	0.29±0.77	-0.46±0.57	-0.62±1.42	-0.23±1.38

Fox Sparrow	*Passerella iliaca*	Canadian	1.12±0.56	-0.43±0.53	1.89±0.64	-3.09±0.58	0.54±0.62	0.46±0.51	0±0.54	-0.32±0.54
Song Sparrow	*Melospiza melodia*	Transition	-1.11±0.54	0.72±0.49	-1.45±0.47	-0.46±0.38	0.5±0.48	-0.01±0.37	0.19±0.49	0.54±0.49
Lincoln's Sparrow	*Melospiza lincolnii*	Canadian	-1.24±0.9	0.1±0.74	4.25±1.24	-2.41±0.85	0.1±0.73	-0.52±0.56	0.16±0.63	-0.3±0.62
White-crowned Sparrow	*Zonotrichia leucophrys*	Hudsonian	-3.31±0.92	-1.01±0.77	4.84±1.46	-0.17±0.91	-0.09±0.72	-0.04±0.55	0.19±0.68	-2.59±0.91
Dark-Eyed Junco	*Junco hyemalis*	Canadian	1.78±0.88	0±0.82	4.47±0.98	-1.11±0.82	0.44±0.72	-0.14±0.59	3.11±1.03	1.41±0.96
Summer Tanager	*Piranga rubra*	Unclassified	-4.62±1.91	0.73±1.06	-3.78±1.78	-1.81±1.09	-0.65±0.8	0.1±0.6	-1.22±1.33	-1.06±1.27
Western Tanager	*Piranga ludoviciana*	Transition	1.99±0.82	0.33±0.75	0.56±0.52	-1.67±0.49	-1.07±0.55	-0.53±0.46	2.45±0.78	1.42±0.61
Black-headed Grosbeak	*Pheucticus melanocephalus*	Upper Sonoran	0.44±0.69	0.02±0.61	-4.27±0.88	-2.22±0.63	-0.4±0.65	-0.38±0.49	1.72±0.7	0.35±0.64
Blue Grosbeak	*Passerina caerulea*	Lower Sonoran	-4.22±1.32	-0.37±0.88	-4.54±1.58	-0.76±0.76	-0.04±0.71	-0.28±0.48	-1.99±0.92	-0.74±0.78
Lazuli Bunting	*Passerina amoena*	Upper Sonoran	-0.18±0.59	0.08±0.57	-2.66±0.61	-0.78±0.54	1.29±0.6	-0.03±0.49	0.57±0.59	-0.4±0.59
Red-winged Blackbird	*Agelaius phoeniceus*	Lower Sonoran	-0.5±0.65	0.52±0.57	-1.86±0.53	-0.02±0.44	0.47±0.54	0.07±0.45	-0.55±0.58	-0.13±0.55
Tricolored Blackbird	*Agelaius tricolor*	Lower Sonoran	-4.35±1.3	0.66±0.94	-2.29±1.26	-0.37±0.82	-0.17±0.72	-0.08±0.51	-0.06±0.93	-1.43±1.1
Western Meadowlark	*Sturnella neglecta*	Lower Sonoran	-1.97±0.78	-0.96±0.68	-3.8±0.87	-0.06±0.69	0.84±0.69	-0.5±0.54	-1.48±0.83	1.87±0.77
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	Transition	-3.34±2.37	-0.26±1.01	-1.12±1.31	0.16±0.79	-0.05±0.74	-0.07±0.52	-1.23±1.36	0.93±1.18
Brewer's Blackbird	*Euphagus cyanocephalus*	Upper Sonoran	0.09±0.61	0.16±0.57	-1.3±0.68	0.94±0.55	-0.12±0.59	0.03±0.5	-0.07±0.53	-0.1±0.53
Great-tailed Grackle	*Quiscalus mexicanus*	Unclassified	-8.21±2.31	0.17±1.1	-2.84±1.76	0.03±0.96	-0.54±0.78	0.54±0.58	-0.98±1.39	0.62±1.18
Brown-headed Cowbird	*Molothrus ater*	Lower Sonoran	-1.38±0.94	2.7±0.87	-2.27±0.79	-0.51±0.56	-0.33±0.7	0.22±0.52	-1.15±0.71	-0.51±0.68
Bullock's Oriole	*Icterus bullockii*	Lower Sonoran	-2.63±1.12	1.11±0.84	-6.16±1.43	-0.55±1.06	-0.7±0.79	0.09±0.61	-0.68±1.04	-0.85±1.05
Gray-crowned Rosy-Finch	*Leucosticte tephrocotis*	Alpine	-7.67±1.83	-0.43±1.01	3.51±1.6	0.7±0.96	0.34±0.76	0.27±0.59	0.77±1	-1.07±1.22
Pine Grosbeak	*Pinicola enucleator*	Hudsonian	-5.74±1.51	0.65±0.98	2.03±1.52	-1.6±0.99	0.5±0.78	-0.04±0.62	1.93±1.13	-0.64±1.28
Purple Finch	*Carpodacus purpureus*	Transition	0.74±0.65	0.56±0.6	0.12±0.5	-2.14±0.55	0.52±0.58	-0.2±0.51	-0.61±0.63	0.51±0.65
Cassin's Finch	*Carpodacus cassinii*	Canadian	-1.62±0.85	0.77±0.68	5.36±1.18	-0.98±1.12	0.39±0.8	0.08±0.62	1.51±0.86	0.66±0.79
House Finch	*Carpodacus mexicanus*	Lower Sonoran	0.33±0.63	-0.95±0.64	-2.69±0.64	0.67±0.59	-0.72±0.65	-0.01±0.55	-2.51±0.8	-1.68±0.72
Red Crossbill	*Loxia curvirostra*	Canadian	-1.46±0.88	1.13±0.75	2.7±1.1	-1.74±0.77	0.51±0.71	0±0.52	-1.66±0.68	-0.41±0.66
Pine Siskin	*Spinus pinus*	Canadian	0.48±0.75	-0.48±0.67	2.39±0.79	0.06±0.67	1.02±0.71	-0.23±0.56	0.33±0.72	-0.17±0.73
Lesser Goldfinch	*Spinus psaltria*	Upper Sonoran	1.1±0.66	0.26±0.53	-2.52±0.58	-0.7±0.55	-0.2±0.58	-0.94±0.51	-1.32±0.61	-0.94±0.57
Lawrence's Goldfinch	*Spinus lawrencei*	Upper Sonoran	-0.61±1.02	0.13±0.85	-3.39±1.02	-0.75±0.85	-0.07±0.73	-0.28±0.61	-1.82±0.96	-1.45±0.98
American Goldfinch	*Spinus tristis*	Lower Sonoran	-7.03±1.29	0.45±0.91	-3.7±1.29	0.13±0.69	0.18±0.71	-0.55±0.49	1.77±0.86	3.35±0.85
Evening Grosbeak	*Coccothraustes vespertinus*	Canadian	-1.93±0.86	-0.08±0.68	0.61±0.69	-2.04±0.64	1.01±0.69	-0.06±0.55	2.75±0.76	3.04±0.77

House Sparrow	*Passer domesticus*	Lower Sonoran	-3.92±1.16	0.31±0.92	-2.75±1.04	0.15±0.67	-0.01±0.69	0.05±0.49	-0.66±0.85	-0.93±0.81

[*] According to the detectability equation: $\operatorname{logit}\left(p_{i,j,k}\right) = \alpha_{0,i} + \alpha_{1,i} era_j + \alpha_{2,i} jday_{j,k} + \alpha_{3,i} jday^2_{j,k}$

And the occupancy equation:

$$\operatorname{logit}\left(\psi_{i,j}\right) = \beta_{0,i} + \beta_{1,i} era_j + \beta_{2,i} elev_j + \beta_{3,i} elev^2_j + \beta_{4,i} era_j elev_j + \beta_{5,i} era_j elev^2_j$$
$$+\beta_{6,i} R1_j + \beta_{7,i} R2_j$$

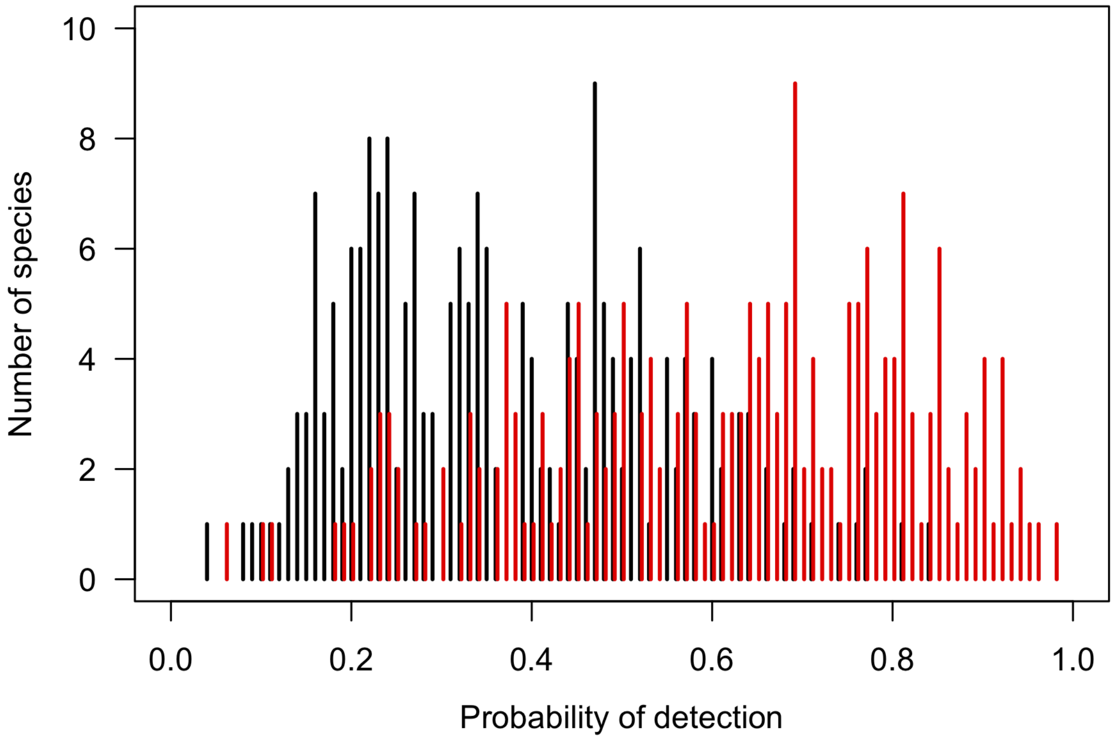


Figure S1. Histograms of frequency of probability of detection for 210 bird species in the historic (black) surveys and the modern (red) surveys. Probabilities are based on the likelihood of seeing a species given one visit to a site at the middle of the breeding season. Histograms are divided into bins with width 0.01, with modern bars offset by 0.005. While the range of species detection probabilities has remained nearly constant, the mean detection frequency is higher in the modern resurveys.

Appendix 1. WinBUGS model specification of multi-species occupancy model.

```
model {

      #PRIORS

      omega ~ dunif(0,1)
      mu.b0 ~ dnorm(0,0.001)
      mu.b1 ~ dnorm(0,0.001)
      mu.b2 ~ dnorm(0,0.001)
      mu.b3 ~ dnorm(0,0.001)
      mu.b4 ~ dnorm(0,0.001)
      mu.b5 ~ dnorm(0,0.001)
      mu.b6 ~ dnorm(0,0.001)
      mu.b7 ~ dnorm(0,0.001)
      mu.a0 ~ dnorm(0,0.001)
      mu.a1 ~ dnorm(0,0.001)
      mu.a2 ~ dnorm(0,0.001)
      mu.a3 ~ dnorm(0,0.001)
      tau.b0 ~ dgamma(0.1,0.1)
      tau.b1 ~ dgamma(0.1,0.1)
      tau.b2 ~ dgamma(0.1,0.1)
      tau.b3 ~ dgamma(0.1,0.1)
      tau.b4 ~ dgamma(0.1,0.1)
      tau.b5 ~ dgamma(0.1,0.1)
      tau.b6 ~ dgamma(0.1,0.1)
      tau.b7 ~ dgamma(0.1,0.1)
      tau.a0 ~ dgamma(0.1,0.1)
      tau.a1 ~ dgamma(0.1,0.1)
      tau.a2 ~ dgamma(0.1,0.1)
      tau.a3 ~ dgamma(0.1,0.1)

      #Set species loop
      for (i in 1:(n+nzeroes)) {

      #Create Priors for speices i from community level prior distributions

      w[i] ~ dbern(omega)
      b0[i] ~ dnorm(mu.b0, tau.b0)
      b1[i] ~ dnorm(mu.b1, tau.b1)
      b2[i] ~ dnorm(mu.b2, tau.b2)
      b3[i] ~ dnorm(mu.b3, tau.b3)
      b4[i] ~ dnorm(mu.b4, tau.b4)
      b5[i] ~ dnorm(mu.b5, tau.b5)
      b6[i] ~ dnorm(mu.b6, tau.b6)
      b7[i] ~ dnorm(mu.b7, tau.b7)
      a0[i] ~ dnorm(mu.a0, tau.a0)
      a1[i] ~ dnorm(mu.a1, tau.a1)
      a2[i] ~ dnorm(mu.a2, tau.a2)
      a3[i] ~ dnorm(mu.a3, tau.a3)

      #Estimation of Z matrix (true occupancy for species i at point j)
      for (j in 1:J) {
            logit(psi[j,i]) <-b0[i]+b1[i]*era[j]+b2[i]*elev[j]+
             b3[i]*elev2[j]+b4[i]*era[j]*elev[j]+b5[i]*era[j]*elev2[j]+
             b6[i]*YO[j]+b7[i]*LA[j]
```

```
      mu.psi[j,i] <- psi[j,i]*w[i]
      Z[j,i] ~ dbern(mu.psi[j,i])

#Estimate detection for species i at point j during sampling period k

      for (k in 1:K[j]) {
            logit(p[j,k,i]) <- a0[i]+a1[i]*era[j]+a2[i]*jday[j,k]+
             a3[i]*jday2[j,k]
            mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
            X[j,k,i] ~ dbern(mu.p[j,k,i])
            }
      }}

#Create loop to determine site-level richness for all species and for
#species in each life zone

for(j in 1:J){
      Nsite[j]<-inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
      N_LS[j]<-inprod(Z[j,1:n],zone_LS[1:n])
      N_US[j]<-inprod(Z[j,1:n],zone_US[1:n])
      N_TR[j]<-inprod(Z[j,1:n],zone_TR[1:n])
      N_CA[j]<-inprod(Z[j,1:n],zone_CA[1:n])
      N_HU[j]<-inprod(Z[j,1:n],zone_HU[1:n])
      N_AA[j]<-inprod(Z[j,1:n],zone_AA[1:n])
      N_XX[j]<-inprod(Z[j,1:n],zone_XX[1:n])
      }

#Create loop for estimating Sørenson similarity index at eat site
#between time periods

for(l in 1:L){
      S[l]<-(2*inprod(Z[H[l],1:n],Z[M[l],1:n]))/
      (sum(Z[H[l],1:n])+sum(Z[M[l],1:n]))
      }

#End model specification
}
```

Chapter 5.

General conclusions

It is a rare opportunity to have access to such a rich and detailed source of historical information such as the bird surveys contained within the field notebooks of Joseph Grinnell and others at the MVZ. Throughout my dissertation, I have sought to use these data to the best of my abilities, capitalizing on their strengths and accounting for their weaknesses. As much insight as I have extracted from the historical surveys, however, I know there is just as much remaining.

Climate change remains an enigmatic subject to research. A century of modern ecological understanding provides a strong framework upon which to build expectations, hypotheses, and theories, yet empirical studies of climate change impacts are frustratingly difficult. The attribution of observed phenomena to climate change continues to challenge researchers. Climate change is also a long and slow process generally requiring research spanning many years or decades – something that takes continuity of mission, sustained funding, and extraordinary foresight. What we learn, from the unsurprisingly messy results, is that our undercarriage of ecological theory remains strong, yet things are never quite as simple as they seem.

Summary of key findings

The general rule of species distributional shifts in montane regions is that species will shift up in elevation. Species are expected to do this because the globe is warming (on average) and species distributions are limited by temperature. As a species' ideal thermal zone shifts up the mountainside, so should the species. My results (Chapters 2 & 3) provide strong support for the ecological theory underpinning this logic, yet clearly illustrate how the simplistic application of the logic fails empirically. As to the theory, species do appear to be tracking their climatic niches through time (Chapter 2). As to the application, species are shifting up (Chapter 3), however almost as many are shifting down, and many more have not shifted at all. This failure of the general rule lies partly in the assumption that a species' range formed by tens to millions of individual occurrences should behave as one unit and respond to averaged regional climate. Rather, an individual animal will respond to the climate it experiences, and tens to millions of individuals experiencing tens to millions of local climates culminates in a range shift. While this research did not focus on individuals, it did show that predictions of range shifts based on the specific climatic history of occupied sites were far more accurate than predictions based on expectations that all species would shift up (Chapter 3). Climate has not changed uniformly in California, and some areas have seen cooling as well as warming. Depending on where species occur, we may expect downward shifts.

Another reason for failure of the general rule is that temperature has largely been the only climatic factor previously considered to be responsible for range shifts. However, a large group of bird species in California, particularly those living at lower elevations, appear to be tracking precipitation over time and moving independently of temperature changes (Chapter 2).

Precipitation also appears to be integral in accounting for many of the observed elevational range shifts of species (Chapter 3). While precipitation is not often considered a proximate limitation on species distributions, the idea that a species' range may be limited by precipitation but not temperature is consistent with Joseph Grinnell's contention that each species' range may be limited at different boundaries by different aspects of its ecological niche. My research provides strong evidence that range shifts for some species are related to non-temperature climatic factors, and it suggests (Chapter 2) that other, unexplored, factors (such as Net Primary Productivity) may play important roles as well.

The cumulative result of species range shifts has unknown consequences on community richness and assembly. In the Sierra Nevada, I found that bird species richness decreased at sites across all elevations, with turnover greatest at the lowest and highest elevations (Chapter 4). Losses appeared greatest for Lower Sonoran, Canadian, and Hudsonian life zone species, while unclassified species (e.g., waterbirds, recent invaders) increased in richness, particularly at low elevations. As there was no universal pattern of range shifts across species (Chapter 3), widespread richness declines suggest range contractions are outpacing range expansions. This has important conservation implications, both in regards to species-specific conservation and community function.

Finally, occurrence data is critical to our understanding of distributions, but comparing occurrence data has numerous obstacles to overcome, primarily resulting from the unavoidable existence of false absences in the data. Occupancy modeling is a powerful and flexible technique for accounting for false absences through the ability to model species-, site-, and survey-specific detection probabilities (Chapter 1). It can also account for problems that are specific to resurveys of historical occurrence data, such as geographic uncertainty in survey location. Occupancy modeling can be used to estimate range shifts (Chapter 3) and to evaluate among factors that relate to the probability of site colonization or extinction (Chapter 2). Accounting for false absences is critical, as analyses conducted on only those species observed can result in skewed or false conclusions (Chapter 4).

Directions for future work

There are many potential avenues for future research building off the work presented in this dissertation. Incorporating the effect of land use change into the evaluation of range changes remains a high priority. Investigating the relationship between occurrence change and other climatic factors, including net primary productivity and climatic water balance, is also of great interest. Ultimately, comparing avian distributional changes to vegetation changes would be of great value although it is uncertain if enough overlapping data will be available to provide insight.

A striking result to come out of this research is the large number of species that have not shifted distributions, despite climatic pressures to do so. These species may deserve additional conservation attention, as range shifting is an adaptation to climate change and species that do not shift may eventually suffer range retractions or localized extinctions. My research suggests a number of reasons why species may not shift. First, I found evidence (Chapter 3) that longer-lived and more behaviorally plastic species may be more likely to shift distributions. Consequently, some species may not have the ability to shift over short time spans, resulting in currently occupied areas becoming ecological sinks as climate becomes unfavorable. Second, species generally experience broader climatic conditions continentally than they do in their California range. Thus, climate may not have shifted enough in California to push species out of their climatic niche (Chapter 2). Additionally, if species in California already inhabit marginal niche space, climate may be moving them toward more favorable conditions (Chapter 2), allowing species to “ride” climate to better conditions without requiring range shifts. These various reasons might alternatively explain why species may not have shifted their range in the Sierra Nevada, yet determining between them may be critical. Targeted research could address each hypothesis directly and thereby help set the appropriate level of conservation concern.

In regards to Chapter 4, I see this chapter as only a first step in understanding the community level consequences of climate change. A larger and unexplored question asks what the impact of range shifts is on species interactions. Are species shifting together as communities? Are novel assemblages being created? A first step would use the gathered occurrence data to explore these questions, but a second step would seek to understand interactions between species. Are newly co-occurring species interacting *in situ*? Is climate change providing new opportunities for inter-species competition? These are critical ecological questions with generally few opportunities for empirical exploration.

Overall, my work brings a spatially broad and temporally long perspective to research on the impacts of climate change on vertebrates. The results contained in this dissertation may only begin to provide insight on the myriad questions surrounding climate change impacts, but they strongly signal where to look next.

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