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By

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Committee in charge:

Professor Steven R. Beissinger, Chair
Professor Laurel G. Larsen
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Abstract

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Anthropogenic climate and land-use change are widely considered to be the two greatest threats to global biodiversity and ecosystem functioning. Although species may respond to changing environments in a variety of ways, the majority of species are expected to shift their distributions to track ecologically favorable habitats. The extent of these shifts may be heterogenous across species or even within a species occupying different regions, but our knowledge of what drives this heterogeneity is still sorely lacking. In particular, the effects of climate and land-use change on shifting species distributions have largely been studied independently. In more realistic scenarios, most species will experience both drivers simultaneously, creating the potential for heterogeneous changes in species composition across regions with different histories of climate and land-use change, as well as species with different sensitivities to that change.

To investigate the combined effects of climate and land-use change on species occupancy and community composition, I surveyed avian diversity at 71 sites in the California Central Valley and Los Angeles. These sites were originally surveyed in the early 1900s by Joseph Grinnell and colleagues from the Museum of Vertebrate Zoology, providing a unique opportunity to directly compare bird occupancy and its relation to site-specific climate and land-use covariates across a century of change. Historic surveys paired with modern resurveys documented changing distributions by 148 bird species across two regions with similar initial species and habitat composition but differing patterns of climate and land-use change.

Our knowledge of species' ecological and life history traits as predictors of sensitivity to land-use change is well developed, but the same cannot be said for traits as predictors of climate-induced range shifts. There is strong theoretical support that range shifts under climate change may be mediated by traits that facilitate dispersal and population establishment, but empirical evidence for this relationship has been mixed. In my first chapter, I conducted a meta-analysis of studies that analyzed climate-induced range shifts as a function of species' traits, with the goal of identifying which traits have provided the strongest results. I show that the majority of traits failed to predict range shifts consistently across studies, while a much smaller number of traits,

particularly habitat breadth, had strong empirical support. In subsequent chapters, I use the most informative species' traits revealed by this meta-analysis to explore differences in species-specific occupancy change across my Central Valley and Los Angeles survey sites.

Both climate and land-use change are expected to favor exotic and generalist species over specialists, resulting in declining occupancy and diversity. Using occurrence data for 122 bird species from 41 resurvey sites in the California Central Valley, my second chapter examined how occupancy and diversity changed over the past 100 years in this predominantly agricultural region, as well as the relative influence of climate versus land-use covariates to occupancy within each survey period. In contrast to expectations that occupancy and diversity would decline, both remained stable: species that increased in occupancy (predominantly habitat generalists or human adapters) roughly balanced species that decreased in occupancy (predominantly open-habitat species), resulting in no significant change in average species richness or between-site diversity. Equally surprising was the far greater importance of water availability (precipitation and water cover) to occupancy within each survey period as compared to urbanization or agricultural cover.

The relative importance of climate versus land-use change to changes in species occupancy is poorly known and may result in heterogeneous patterns of diversity change across regions with different climate and land-use change histories. In my third chapter, I used occurrence data for 148 bird species across the full set of 42 Central Valley sites and 29 Los Angeles sites. I directly assessed the relative importance of climate and land-use covariates to probabilities of occupancy, persistence, and colonization, as well as compared patterns of occupancy and diversity change between the two regions. Climate and land-use covariates were both important, but to different aspects of occupancy and turnover, with climate driving initial occupancy, climate and land-use both having similar influence on colonization, and urban cover emerging as the biggest driver of local persistence. In contrast to stability in occupancy and diversity in the Central Valley, both declined in Los Angeles. This diversity loss resulted from a greater amount of urban development in Los Angeles and larger species-specific occupancy decreases in particularly forest and open-habitat species.

Overall, my dissertation provides a detailed picture of how bird species have responded to over a century of climate and land-use change. These changes were highly heterogeneous across species – driven by traits, namely habitat preference – and across very similar ecological regions – driven by divergent patterns in both climate change and urbanization. As we continue to create range projections and plans to conserve future diversity, it will be important to utilize knowledge generated by long-term historical datasets and to incorporate multiple drivers of heterogeneity in species' responses to global change.

To my parents, Wendy and John, and to my Nathan

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Chapter 1.

Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis

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Abstract

A growing body of literature seeks to explain variation in range shifts using species' ecological and life history traits, with expectations that shifts should be greater in species with greater dispersal ability, reproductive potential, and ecological generalization. Despite strong theoretical support for species' traits as predictors of range shifts, empirical evidence from contemporary range shift studies remains limited in extent and consensus. We conducted the first comprehensive review of species' traits as predictors of range shifts, collecting results from 51 studies across multiple taxa encompassing over 11,000 species' responses for 54 assemblages of taxonomically-related species occurring together in space. We used studies of assemblages that directly compared geographic distributions sampled in the 20th century prior to climate change with resurveys of distributions after contemporary climate change, and then tested whether species traits accounted for heterogeneity in range shifts. We performed a formal meta-analysis on study-level effects of body size, fecundity, diet breadth, habitat breadth, and historic range limit as predictors of range shifts for a subset of 21 studies of 26 assemblages with sufficient data. Range shifts were consistent with predictions based on habitat breadth and historic range limit. However, body size, fecundity, and diet breadth showed no significant effect on range shifts across studies, and multiple studies reported significant relationships that contradicted predictions. Current understanding of species' traits as predictors of range shifts is limited, and standardized study is needed for traits to be valid indicators of vulnerability in assessments of climate change impacts.

Introduction

Although species' functional traits have long been recognized as being both products and drivers of ecological processes (Stearns 1977, Tilman et al. 1996), a renewed focus on trait diversity has grown in recent years (Gibert et al. 2015). Ecological and life-history traits shared by groups of organisms have been used to create frameworks for community assembly (Laughlin et al. 2012) and nutrient cycling (Zuo et al. 2015), predict species and community responses to disturbance (Mouillot et al. 2013, Pellegrini et al. 2016, Pryde et al. 2016), and evaluate ecosystem functions and services (Cardinale et al. 2012, Schmitz et al. 2015). Species' traits are also well-known drivers of invasion ecology and range dynamics (Clark 1998, Chuang and Peterson 2016), making them promising candidates to explain species-specific variation in range shifts under contemporary climate change (Estrada et al. 2016).

Range shifts observed under recent climate change appear highly idiosyncratic (Parmesan and Yohe 2003, Wiens 2016), and are thought to be driven by exposure (as measured by the magnitude of climate change experienced by a species; Loarie *et al.* 2009; Dawson *et al.* 2011) and mediated by species-specific capacities to move to more suitable locations (Williams et al. 2008, Dawson et al. 2011). Traits have important influences on how species respond to exposure and their range expansion capacity. Therefore, traits could provide valuable evidence-based tools for conservation and management that could increase the accuracy of extinction risk projections (Thomas et al. 2004, La Sorte and Jetz 2010), vulnerability assessments (Foden et al. 2013, Foden and Young 2016), and predictions of novel community assemblages (Williams and Jackson 2007, Stralberg et al. 2009).

Hypotheses for how species' traits should relate to range shifts are based largely on assumptions that patterns will be similar to those observed in studies of abundance shifts, range size, range filling, and invasion potential (Estrada et al. 2016). For the margin of a species' range to expand, individuals must possess the physical capacity to disperse into previously unoccupied areas. Therefore, species with greater dispersal potential (e.g., larger body size or more migratory behavior) are expected to show larger range shifts (Angert et al. 2011, Buckley and Kingsolver 2012). Once individuals of a species disperse into previously unoccupied areas, high reproductive potential (e.g., fast life history strategies such as high fecundity and low longevity) facilitates the establishment of viable populations (Perry et al. 2005, Angert et al. 2011). Persistence in areas beyond the historic range limit will also depend on the ability to find appropriate food and habitat. Generalist species (e.g., those with greater diet or habitat breadth) should be more likely to find suitable resources in novel areas and should therefore show greater range shifts than specialists, which require concomitant range shifts of species on which they depend (Berg et al. 2010, Angert et al. 2011, Buckley and Kingsolver 2012). Finally, though not strictly a species' trait, species with initial range limits located at higher latitudes or altitudes are expected to show smaller range shifts over time; for example, mountaintop species have less room to shift their altitudinal limit upward (Angert et al. 2011).

Despite strong theoretical support for these traits as predictors of climate-induced range shifts, empirical support is limited in extent and consensus (Angert et al. 2011, Buckley and Kingsolver 2012). At the species and community scales, considerable controversy remains over the mechanistic justification for traits (Estrada et al. 2016), particularly under varying contexts of environmental matching (Sol et al. 2012), biotic interactions (Angert et al. 2011), and trait covariance (Sekar 2012, Laube et al. 2013). At broader geographic and taxonomic scales, traits are increasingly being incorporated into multispecies range projections (Midgley et al. 2006, Iverson et al. 2011, Schloss et al. 2012, Barbet-Massin et al. 2012, Bateman et al. 2013) and climate change vulnerability assessments (Gardali et al. 2012, Foden et al. 2013, McClure et al. 2013). Such models may provide a useful approximation of heterogeneity in species-specific range shifts when mechanistic data are not available or feasible to incorporate (Buckley and Kingsolver 2012), but they assume trait-based relationships that at present remain largely unvalidated. Recently Pacifici et al. (2017) examined if life history traits explained whether bird and mammal populations were positively or negative affected by climate change, but there has been no global analysis of how traits influence recent range shifts of species.

Two approaches can be used to quantitatively synthesize the strength of current evidence for traits as predictors of recent range shifts. The first approach is to conduct a meta-analysis of primary data (Mengersen et al. 2013a) compiled from existing studies of range shifts of individual species and their corresponding traits to produce a fine-scale investigation of the influence of traits in different phylogenetic, geographic, and biotic contexts. While meta-analysis of primary data is often championed, valid applications must address problems of comparability among studies due to ecological and methodological heterogeneity, and it is often difficult, costly, and time-consuming to assemble a comprehensive and comparable dataset with all of the relevant data (Mengersen et al. 2013a). As a result, meta-analyses of primary data are rare in ecology (Mengersen et al. 2013a) as well as in the data-rich field of medicine (Simmonds et al. 2005). To the best of our knowledge, a data set compiling range shifts of species related to contemporary climate change and their corresponding traits does not currently exist.

The second approach is to conduct a formal meta-analysis of study-level effect sizes for aggregated data from published studies that compared geographic distributions of assemblages (taxonomically-related species occurring together in space; Stroud *et al.*, 2015) sampled in the 20th century prior to climate change with resurveys of distributions after contemporary climate change, and then tested whether species traits accounted for heterogeneity in range shifts. Meta-analysis of aggregated data encompasses a set of rigorous statistical techniques (Glass 1976, Koricheva and Gurevitch 2013) that have been used to synthesize evidence for over three decades in the social sciences (White 1982, Hines et al. 1987) and over two decades in ecology (Jarvinen 1991, Myers and Mertz 1998, Aguilar et al. 2006, McKnight et al. 2016, Weber et al. 2016). These methods estimate the mean effect size across multiple studies after weighting individual studies by their standard error (i.e., stronger studies with smaller standard errors weight more heavily), and can be designed to account for ecological and methodological heterogeneity among studies using covariates (Stewart et al. 2013).

Here we evaluate empirical support for the leading hypotheses that climate-induced range shifts are larger in species with greater dispersal ability, reproductive potential, and ecological generalization (Angert et al. 2011, Buckley and Kingsolver 2012, Estrada et al. 2016). We present the first comprehensive review of species' traits as predictors of recent range shifts, using vote-counting to summarize results from 51 studies encompassing over 11,000 species responses across 54 assemblages of multiple taxa. We then conduct a formal meta-analysis to quantitatively assess study-level mean effect sizes on range shifts for five focal traits with sufficient sample sizes – body size, fecundity, diet breadth, habitat breadth, and historic range limit. This two-step procedure of vote counting followed by formal meta-analysis is recommended to avoid a loss of information (Koricheva & Gurevitch, 2013, page 11). Our meta-analysis objectives were to (i) calculate the mean effect size of each trait on observed range shifts, and (ii) test whether study-level ecological and methodological covariates explain variation in effect sizes of traits across studies. While our meta-analysis is unlikely to control for all sources of heterogeneity among studies, it provides an informative first assessment of traits as predictors of climate-induced range shifts at the broad taxonomic and geographic scales currently used to project future ranges and to conduct vulnerability assessments for scenarios of climate change.

Methods

We searched the literature for studies that related species' traits to range shifts (either range margin or range center) for assemblages of any taxa. We searched the online database Web of Science for papers published between 2000 and 2015 with keywords "climate" and "range shift/expansion", "latitudinal shift/expansion", or "elevational shift/expansion". The search produced approximately 11,200 results. From this set we chose papers for closer scrutiny if they directly analyzed potential range shifts by explicitly comparing 20th century and contemporary assemblages. These studies included both single-year resurvey efforts and multi-year resurveys of atlas data; for the latter studies, we compared the first and last years of atlas data. Of the 145 papers that met the above criteria, 50 studies (54 analyses of assemblages, accounting for studies that performed separate analyses for different taxa) measured the effect of at least one species trait on variation in range shifts (see Table S1 in Supporting Information). While it would have been ideal to further refine studies to those that accounted for differences in detection probability or survey effort that could bias observed range shifts between 20th century and contemporary surveys, the limited number of studies (Moritz et al. 2008, Tingley et al. 2009) made this unfeasible.

We began analysis by qualitatively summarizing results (significant positive, significant negative, or nonsignificant) for the eight most commonly tested traits across studies: body size, migratory strategy, movement ability (including seed dispersal mode, flight behavior, or dispersal distance), fecundity, longevity, diet breadth, habitat breadth, and historic range limit. We then carried out meta-analyses for five focal traits that were measured consistently by at least six studies: body size (13 studies; 13–1075 species/study), fecundity (9 studies; 13–143 species/study), diet breadth (14 studies; 13–282 species/study), habitat breadth (10 studies; 13–1075 species/study), and latitudinal or altitudinal limit of the historic range (8 studies; 13–143 species/study). Raw data on effect sizes are given in Tables S2-S6 in Supporting Information.

Body size was quantified as average length or mass, and fecundity as the number of eggs or live young produced annually per female. Most studies quantified diet breadth and habitat breadth using a discrete numerical scale that represented the number of diet or habitat types used by a species; for studies that presented only categorical diet or habitat categories, we reduced the data to a binary comparison between the omnivore or generalist category (as identified by the original study) and any other categories. Studies documented shifts in the margin (n = 22 with 7-13 studies per trait) or center (n = 4 with 0-1 studies per trait) of either elevational (n = 13 with 4-5 studies per trait) or latitudinal (n = 13 with 3-9 studies per trait) ranges and encompassed a variety of taxa and geographic locations (Figure S1). Migratory strategy, movement ability, and longevity traits were included in our literature review and a vote-count tally of studies evaluating predictions but could not be included in our formal meta-analysis due to insufficient sample size or non-comparable trait measurement schemes across studies.

For each study, we collected an effect size that measured the trait's influences on range shifts for assemblages of taxonomically-related species. Studies varied in how they measured traits (e.g., mass or length for body size) and range shifts (e.g., distance of shift, rate of shift, or a binary shift v. no shift), so we standardized all effect sizes. For categorical trait variables, we calculated the standardized mean difference in range shifts between two groups (e.g., omnivores versus specialists) using Cohen's D (Lipsey and Wilson 2001, Rosenberg et al. 2013). For continuous variables, we used the beta coefficient reported from regression analysis. When standardized beta coefficients were not provided in the original study, we standardized the coefficients following Bring's (1994) equation:

$$\beta_s = \beta_{us} \frac{\sigma_x}{\sigma_y}$$

where β_s = the standardized beta coefficient, β_{us} = the unstandardized beta coefficient, σ_x = the standard deviation of the raw trait data, and σ_y = the standard deviation of the raw response data. In other words, the standardized beta coefficient quantifies how a change in *x* standard deviations of a trait variable is expected to produce a change of *y* standard deviations in extent of a range shift.

To explore sources of heterogeneity that may influence effect size, we compiled a set of study-level covariates related to both ecological and methodological factors. Ecological factors included taxa mobility (mobile birds and marine fish versus other, less mobile taxa, with grouping based on patterns observed in the literature review; a full taxa-based analysis was impractical due to limited sample size) and range shift type (latitudinal or altitudinal). A covariate to control for whether a study analyzed the range center versus margin was not feasible because only four studies quantified shifts in range centers. Visual inspection of the standardized effect sizes and variances for those four studies (Perry et al. 2005, Nye et al. 2009, Forero-Medina et al. 2011, Reif and Flousek 2012) indicated that they were within the values spanned by studies of range margins. Methodological factors included the number of species studied, study duration (number of years between historic and modern data), exposure to climate change (change in mean annual temperature over the study period; when not reported, we calculated change in mean annual temperature between the first and last ten years of the study using WorldClim data; Hijmans *et al.*, 2005), size of study area (km^2), and phylogenetic control (a binary indicator of whether or not a study controlled for phylogeny in the analysis). The latter is a reasonable approach given that meta-analytical methods cannot fully control for phylogeny, especially in our study where effect size is unable to be decomposed and taxa are so diverse that combining phylogenies would be difficult (Jennions et al. 2013, Lajeunesse et al. 2013).

We analyzed effect sizes using the metafor package in R (Viechtbauer 2010, Schmid et al. 2013). We used meta-analysis models to calculate mean effect size across studies by weighting each study-specific effect size by its corresponding standard error. We used random effects (RE) models that allowed effect sizes to vary around the mean due to unaccounted for heterogeneity in methodology or study system (Mengersen et al. 2013b). We used RE models as opposed to fixed effects models, because the latter assume a single common effect size across studies and assume that any heterogeneity across studies is due to chance alone (Trikalinos et al. 2008, Viechtbauer 2010).

To calculate mean effect sizes, we modelled each trait individually without covariates to test whether the mean effect size across studies was significantly different from zero. Although a multivariate framework may be ideal to calculate the relative effects of and potential interactions among traits, the univariate approach was a limitation of our meta-analysis model and the small number of studies that analyzed similar sets of traits (see also McKnight *et al.*, 2016). We also modelled effect size as a function of study-level covariates to explore drivers of heterogeneity across studies and to determine whether mean effect sizes were significantly different from zero when accounting for this variation. We present model sets consisting only of individual covariates; complex models consisting of additive combinations of two covariates and interactive effects between methodological and ecological covariates were not included in the model set due to limited sample size and to avoid overfitting. Exploratory analyses indicated that models with combinations of two or more covariates never performed better than models with one covariate. Model code is provided in Appendix 1 of Supporting Information.

We assessed publication bias through visual inspection of funnel plots, a scatterplot of effect size against standard error (Jennions et al. 2013). Although funnel plots are difficult to interpret when fewer than 30 studies are included (Jennions et al. 2013), funnel plots from the top model for each trait were relatively evenly and symmetrically distributed (Figure S2). Additionally, the mean range shifts from studies included in our meta-analysis had a similar median and range when compared to the mean range shifts reported in the other studies of assemblages we identified in our literature review (Figure S3).

Results

Figure 1 summarizes qualitative results for the eight most commonly-tested traits (from 5439 species responses across 39 studies of 42 assemblages). The relationship between traits and range shifts varied greatly among studies. Significant effects were uniformly positive for habitat breadth and for traits related directly to movement ability (including seed dispersal mode or natal dispersal distance). Significant effects were uniformly negative for historic range limit. Migratory strategy, fecundity, longevity, diet breadth, and body size exhibited a mixture of significant positive and negative relationships with range shifts. When considering both significant and non-significant results, historic range limit was the strongest predictor of range shifts, with 60% of studies upholding the prediction that range shifts should be negatively related to historic range limit. Predicted relationships between traits and range shifts were weakly to moderately upheld for dispersal ability (22% for studies of body size, 10% for migratory strategy, and 50% for movement ability), reproductive capacity (36% for fecundity and 60% for longevity), and ecological generalization (27% for diet breadth and 43% for habitat breadth).

In the formal meta-analysis (based on 3123 species responses across 21 studies of 26 assemblages), effect sizes varied greatly among studies and included both positive and negative effects for all traits except historic range limit (Fig. 2). Mean effect size did not differ significantly from zero for body size, fecundity, diet breadth, or habitat breadth (Table 1, Fig. 1), indicating that these traits did not have a significant effect on range shifts across studies. However, historic limit had a significant mean effect size of −0.30 ($\tau^2 = 0.037$; 95% CI = −0.48,

−0.12), indicating that for every standard deviation increase in latitude or altitude of the historic range limit of a species, its corresponding range shift decreased by 0.3 standard deviations.

Ecological and methodological differences among studies accounted for heterogeneity in effect sizes of some traits. Variation in effects of body size was best explained by taxa mobility (Table 2). Body size had a significantly negative mean effect on range shifts of birds and marine fish ($\mu = -0.275$, 95% CI = −0.45, −0.01), indicating that range shifts increased as body size decreased. In less mobile taxa, body size explained little variation in range shifts (Fig. 2a; $\mu = 0.148$, 95% CI = −0.07, 0.36). Mean effect size of diet breadth (Fig. 2c) was best explained by whether the range limit studied was altitudinal ($\mu = -0.23$, 95% CI = −0.48, 0.02) or latitudinal ($\mu = 0.08$, 95% CI = −0.06, 0.22), but mean effect sizes for these two groups did not differ significantly from zero (Fig. 2c). Heterogeneity in mean effect size of habitat breadth was best explained by study area (Table 2); effect size increased as study area increased, with a positive relationship between habitat breadth and range shifts for study areas above 200,000 km^2 (Fig. 2f). Results were unchanged when the largest study area (South Africa, 1.2 million km^2) was excluded from the analysis (AIC_c *w* of top model declined from 0.99 to 0.78). Covariates explained little variation in mean effect sizes of fecundity or historic range limit (Table 2).

Discussion

Degree of support for investigated traits as predictors of recent range shifts

Results from our literature review and meta-analysis indicated that ecological and life history traits had limited success in accounting for variation among species in range shifts over the past century. Predicted relationships between traits and range shifts received only low to moderate levels of support (Fig. 1). Of the five traits that received sufficient study to be included in our formal meta-analysis, only habitat breadth and historic range limit supported range shift predictions (Figs. 1 and 2). All published significant relationships between habitat breadth and range shifts were positive (Pöyry et al. 2009, Hockey et al. 2011, Davey et al. 2013, Powney et al. 2013, Jiménez-Alfaro et al. 2014, Alofs et al. 2014). Although the mean effect size of habitat breadth across all studies did not differ significantly from zero (Fig. 1), range shifts increased with habitat breadth when we accounted for heterogeneity in size of study areas (Fig. 2f). Our meta-analysis also found a significant negative mean effect size between historic range limit and range shifts (Fig. 1), and all published significant relationships were negative (Nye et al. 2009, Angert et al. 2011, Menéndez et al. 2013, Auer and King 2014, Alofs et al. 2014, Grenouillet and Comte 2014). Thus, species that occupied higher altitudes or latitudes tended to have smaller range shifts than species occupying lower altitudes or latitudes.

Some traits showed relationships that were contrary to range shift expectations under the leading hypotheses (Fig.1). Although species with longer migration distances typically have longer dispersal distances (Paradis et al. 1998, Dawideit et al. 2009) and should show greater range shifts, multiple studies have documented smaller range shifts in long-distance migrants compared to short-distance migrants (Brommer 2008, Brommer and Møller 2010, Tingley et al. 2012) or to non-migratory species (Zuckerberg et al. 2009, Tingley et al. 2012). A potential problem with using migratory behavior (and other proxy traits discussed in this paper) as a predictor of range shifts is that other traits associated with long-distance migration may have confounding effects. For example, long-distant migrants often show high fidelity to breeding and overwintering sites (Bensch 1999, Laube et al. 2013), and may be more likely to exhibit phenological shifts in response to climate change (Parmesan and Yohe 2003, Estrada et al. 2016).

Some traits showed no consistent relationship with range shifts. Fecundity and longevity both had a relatively even mixture of significant positive, significant negative, and nonsignificant relationships (Fig. 1), and fecundity did not have a significant mean effect size in the meta-analysis. For diet breadth, relationships with range shifts were insignificant about as often as they were significant (Fig. 1), and significant relationships were equally positive (Angert et al. 2011, Betzholtz et al. 2013, Freeman and Class Freeman 2014, Sunday et al. 2015) and negative (Brommer 2008, Brommer and Møller 2010, Auer and King 2014). Given these contradictory results, it is unsurprising that our meta-analysis found a mean effect size of zero for diet breadth in models both with and without covariates (Tables 1 and 2). Although species with greater diet breadth are predicted to have larger range shifts, an alternative hypothesis is that specialist species may be more likely to shift their ranges as they track their required resources, whereas generalists can persist better *in situ* (Buckley and Kingsolver 2012, Jarzyna et al. 2015).

Body size also showed no significant mean effect size in relation to range shifts across studies of mammals, invertebrates, plants, reptiles, and freshwater fish, but smaller species of birds and marine fish tended to have greater range shifts than larger species (Figs. 1 and 2). Larger-bodied organisms tend to disperse farther than smaller species (Sutherland et al. 2000, Jenkins et al. 2007, Dawideit et al. 2009, Sekar 2012), and fossil data suggests that larger species exhibited greater range shifts in response to glacial-interglacial cycles of the Pleistocene (Kaustuv et al. 2001, Lyons et al. 2010). Therefore, larger species should show greater range shifts in response to contemporary climate change (Angert et al. 2011). However, body size is typically inversely correlated with reproductive potential, and would therefore be expected to show a negative relationship with range shifts (Perry et al. 2005), creating confounding effects.

Limitations of our meta-analysis

Our meta-analysis provides a glimpse of the potential to make important inferences by bringing together disparate studies of range shifts and traits, but was limited in several ways. Some traits have consistently supported the leading hypotheses, but have been tested by too few studies to enable a formal meta-analysis (Fig. 1). For example, larger range shifts occurred in plant species with wind dispersed seeds compared to those with seeds dispersed by animals or gravity (Holzinger et al. 2007, Parolo and Rossi 2008, Felde et al. 2012), in specialist butterflies with more nitrogen-rich diets (Betzholtz et al. 2013), and in birds with larger brain mass (Brommer and Møller 2010). Significant variation in range shifts has also been reported among species belonging to different diet guilds (Brommer 2008, Reif and Flousek 2012, Freeman and Class Freeman 2014), or occupying different habitat niches (Pöyry et al. 2009, Hockey et al. 2011, Angert et al. 2011, Reif and Flousek 2012), but methodological differences in defining these groups prohibited us from calculating effect sizes or making cross-study comparisons. While the current leading hypotheses relating species' traits to range shifts provide a good starting point, they must be expanded to include additional traits as well as alternative competing hypotheses for the effects of traits.

Lack of strong mean effect sizes in our meta-analysis could be due to heterogeneity among studies that was not modeled, such as differences in species' detectability or barriers to movement. Detection probability varies among species, sites, and observers (MacKenzie et al. 2002, Iknayan et al. 2014, Jarzyna and Jetz 2016), and studies that do not control for detection probability may produce biased estimates of range shifts or have little power to detect them (Tingley and Beissinger 2009). However, few studies of range shifts have explicitly modelled the detection process (Moritz et al. 2008, Tingley et al. 2009, 2012). The presence of anthropogenic land-use change in the study area may introduce additional bias in measures of range shifts, particularly if land-use change limits the areas where species can expand to track favorable climate (Jetz et al. 2007, Hof et al. 2011, Nuñez et al. 2013). Species interactions may provide additional biotic barriers to movement through dependence on concomitant shifts in symbiotic species (Araújo and Luoto 2007, Schweiger et al. 2008).

Heterogeneous effect sizes could also be due to methodological variation in the quantification of both traits and range shifts (Brown et al. 2016). Our meta-analysis included studies of both range margins and range centers, and the small sample size of the latter group precluded using range type as a covariate for comparisons of mean effect sizes. It is possible that some traits may better explain shifts at the range margin versus center (Angert et al. 2011), or in portions of the range where shifts are more probable due to heterogeneous climate change velocities (Loarie et al. 2009), but these relationships require further testing. Range shifts were measured in a variety of ways (magnitude of shift, rate of shift, or shift versus no shift) and methods to standardize measurements of range shifts have been proposed (Brommer and Møller 2010, Angert et al. 2011). To our knowledge there have been no studies that have evaluated which range response variable is most suitable for testing against species' traits. Finally, choice of traits, measurement, and categorization varied greatly across studies. For example, none of the six studies of diet guild in birds used the same set of guilds, making cross-study comparison difficult. Moreover, studies investigating the influence of migratory distance failed to find a significant difference in range shifts between migratory and non-migratory bird species (Angert *et al.*, 2011), but significant results emerged when short- versus long-distance migrants were compared (Brommer 2008, Zuckerberg et al. 2009, Tingley et al. 2012). The growing coverage of global trait databases, such as TraitNet (traitnet.ecoinformatics.org), Elton Traits (Wilman et al. 2014), and the TRYplant trait database (www.try-db.org), will facilitate standardization of trait data, but future analyses should also include trait sets that are comparable to other studies. Further complications in quantifying traits may arise due to trait variation within a population, particularly if individuals at an expanding range edge have different traits than individuals in the range center (Bowler and Benton 2005, Krause et al. 2016, Chuang and Peterson 2016).

Conclusions and future directions

The diverse relationships between species' traits and range shifts that we found raise a key question: Are the species' traits that have been studied thus far useful predictors of variation in range shifts? Although some of our results support this assertion, most traits examined in the studies that we analyzed yielded no significant relationships (Fig. 1; Table S1). Even for those relationships that were significant, little variation was explained by traits (3-6% in some studies), which led Angert *et al.* (2011) to conclude that the power of species' traits to predict range shifts is too low to be useful for conservation or management. Low predictive ability when regressing a trait or limited group of traits against range shifts is not necessarily surprising, given the complexity with which traits potentially influence shifts. Nevertheless, some studies have accounted for up to 40-60% of the variation in range shifts using species' traits (Brommer 2008, Alofs et al. 2014). The well-documented importance of traits to other range shift processes, such as invasion or range expansion, provides a strong theoretical justification for their inclusion in studies of range shifts induced by contemporary climate change (Estrada et al. 2016).

We advocate a middle ground between these two views. It may be premature to conclude that species' traits do not have sufficient predictive power to be a useful proxy for range projections and management decisions. Our results suggest that at least two species' traits, habitat breadth and historic range limit, consistently described variation in range shifts across studies spanning diverse taxa and geographic locations, although considerable heterogeneity in effect sizes remains unexplained. However, our results also indicate that the evidence to date is equivocal or unsupported for the role of most leading traits—body size, migration strategy, movement ability, fecundity, longevity and diet breadth—as predictors of recent range shifts. Many more traits remain to be tested. Clearly, much work is still needed to identify the traits best suited to predicting variation in range shifts, and to better understand the influences of taxonomic, geographic, and methodological factors on trait effect sizes.

One approach that might better illuminate how species' traits modify range shifts is to investigate movements relative to niche tracking (Tingley et al. 2009). Our analysis considered only expansions in the poleward or upper elevational range margin, as analyses of other margins are comparatively sparse. However, heterogeneous change in climatic variables related to temperature and precipitation may cause some species to move in counterintuitive directions to track favorable climate (Crimmins et al. 2011, Tingley et al. 2012, Wolf et al. 2016). Species' traits may be stronger predictors of range shifts when investigated in the context of niche tracking and environmental matching (Sol et al. 2012, Wittmann et al. 2016, Wogan 2016). For example, temperature and water flow preference of invertebrates in New South Wales explained whether range shifts occurred at warm versus wet range edges (Chessman 2012).

Phylogenetic context is also an important consideration when evaluating species' responses to global change (Jarzyna and Jetz 2016), and strong phylogenetic biases have been documented for processes such as phenological shifts (Davis et al. 2010). More closely related species typically share more similar traits (Losos 2008), so the relationship between traits and range shifts should have a phylogenetic signal (Pöyry et al. 2009, Angert et al. 2011). However, our meta-analysis found no differences in effect sizes between studies that did and did not control for phylogenetic relatedness. Within-study evaluation of phylogenetically-corrected analyses have produced similar results, at least at the taxonomic level of order (Angert et al. 2011, Auer and King 2014). The phylogenetic signal of range change remains unclear, and will be an important area of future study as a control for, or alternative to, trait-based analysis of range shifts.

Finally, not all species will need to undergo range shifts in order to persist under changing climatic conditions. Numerous studies have documented species responding to changes in their environment through phenotypic plasticity, particularly shifts in phenology (Parmesan and Yohe 2003). Traits such as ecological generalism, may help species temporarily persist *in situ* under changing environmental conditions (Dawson et al. 2011, Buckley and Kingsolver 2012). Relative to range shifts, phenological shifts can be predicted more strongly by traits (Buckley and Kingsolver 2012). Despite the short time frame over which contemporary climate change has taken place, some populations have also shown genetic changes suggestive of evolutionary adaptation (Bradshaw and Holzapfel 2006, Hoffmann and Sgrò 2011). An ideal framework for predicting variation in range shifts should include the combined effects of niche tracking through space or time, plasticity or acclimation, evolution, and species' traits, with choice of traits based on a mechanistic framework such as that developed by Estrada *et al.* (2016).

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Table 1: Mean effect sizes and between-study variation (τ^2) modelled for each trait using random effects models without covariates. For each study trait the number of studies of assemblages used for the meta-analysis, number of species per study (mean ± sd), and total number of species responses pooled across studies are summarized. Number of studies included in meta-analysis is lower than studies reported in vote-counting (Figure 1) because effect sizes could not be obtained from all studies.

Trait	Studies	Species per study	Total responses	Mean effect size	τ^2	SE	$p \leq$
Body size	13	164 ± 283	2131	-0.032	0.128	0.11	0.77
Fecundity	9	67 ± 46	546	0.042	0.034	0.07	0.55
Diet breadth	14	95 ± 77	1323	0.000	0.033	0.07	0.99
Habitat breadth	10	187 ± 324	1863	0.068	0.049	0.09	0.45
Historic range limit	8	52 ± 44	416	-0.300	0.037	0.09	0.001

Table 2: Summary of covariates explaining variation in effect sizes of species traits as predictors of range shifts. For each model, we report τ^2 (variation not accounted for by covariates), ΔAIC_c, and *w* (AIC_c weight). Models with $\Delta AICc < 2$ for each trait are bolded.

	Body Size			Fecundity			Diet Breadth		
Covariates modelled	τ^2	ΔAICc	*w*	τ^2	ΔAICc	*w*	τ^2	ΔAICc	*w*
Exposure (Δ °C)	0.142	7.02	0.02	0.036	4.20	0.07	0.039	3.71	0.05
Number of species	0.144	7.24	0.02	0.039	4.86	0.05	**0.029**	**1.87**	**0.12**
Phylogenetic control	0.139	6.78	0.03	0.039	4.76	0.05	0.038	3.54	0.05
Range type	0.139	6.80	0.03	0.040	5.06	0.05	**0.021**	**0.00**	**0.32**
Study area	0.146	7.34	0.02	0.039	4.86	0.05	0.038	3.57	0.06
Study duration	0.145	7.30	0.02	0.034	3.85	0.09	0.038	3.50	0.06
Taxa mobility	**0.073**	**0.00**	**0.74**	0.038	4.53	0.06	0.031	2.33	0.10
No covariates	0.128	3.45	0.13	**0.034**	**0.00**	**0.58**	**0.033**	**0.43**	**0.25**

	Habitat Breadth			Historic Range Limit		
Covariates modelled	τ^2	ΔAICc	*w*	τ^2	ΔAICc	*w*
Exposure (Δ °C)	0.052	13.67	0.00	0.043	5.31	0.03
Number of species	0.056	14.19	0.00	**0.015**	**1.13**	**0.26**
Phylogenetic control	0.041	12.35	0.00	n/a	n/a	n/a
Range type	0.036	11.60	0.00	0.022	2.46	0.29
Study area	**0.000**	**0.00**	**0.99**	0.029	3.54	0.08
Study duration	0.063	14.91	0.00	0.048	5.83	0.03
Taxa mobility	0.059	14.47	0.00	0.048	5.81	0.03
No covariates	0.049	10.04	0.01	**0.037**	**0.00**	**0.45**

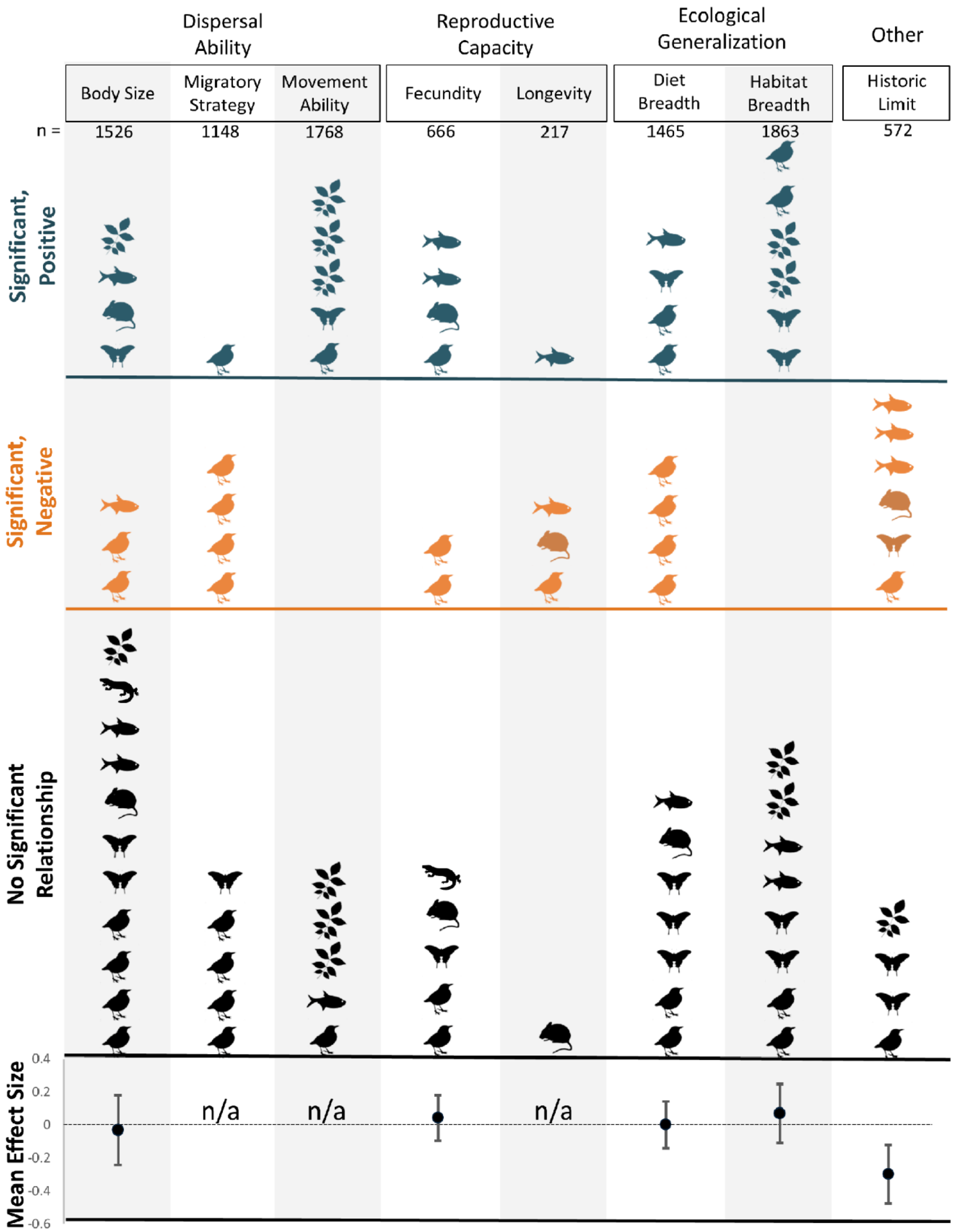

Figure 1. Summary of effects of species' traits on range shifts for the eight most commonly tested traits. Each icon represents the result from a single study of birds, small mammals, fish, invertebrates, reptiles, or plants, respectively, and *n* = the total number of species responses represented by all studies for each trait. Mean effect sizes (± 2 standard errors) are based on meta-analytical models without covariates (see Table 1 for meta-analysis sample sizes).

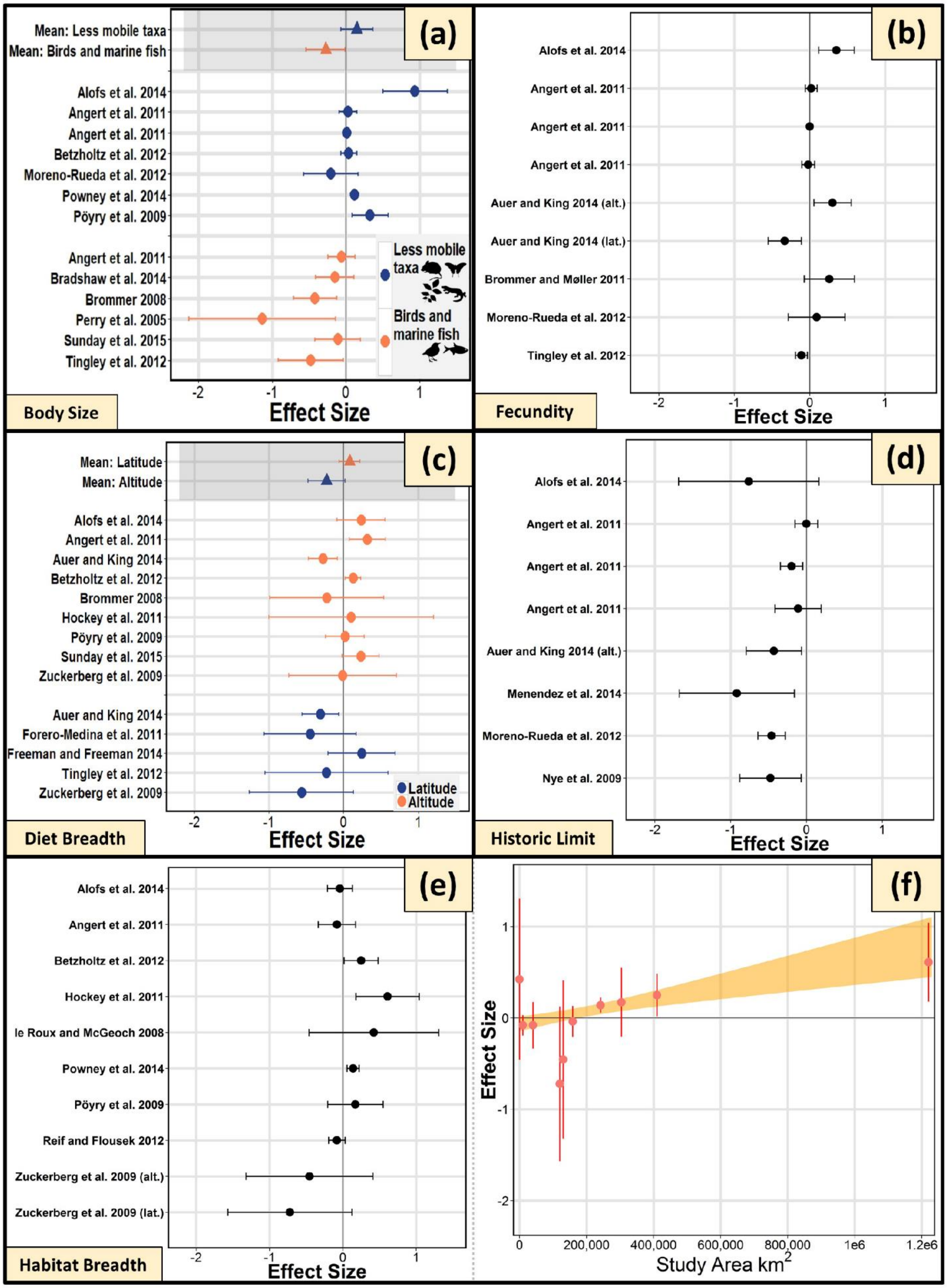
(a)
Mean: Less mobile taxa
Mean: Birds and marine fish
Alofs et al. 2014
Angert et al. 2011
Angert et al. 2011
Betzholtz et al. 2012
Moreno-Rueda et al. 2012
Powney et al. 2014
Pöyry et al. 2009
Angert et al. 2011
Bradshaw et al. 2014
Brommer 2008
Perry et al. 2005
Sunday et al. 2015
Tingley et al. 2012
Less mobile taxa
Birds and marine fish
-2
-1
0
1
Effect Size
Body Size
(b)
Alofs et al. 2014
Angert et al. 2011
Angert et al. 2011
Angert et al. 2011
Auer and King 2014 (alt.)
Auer and King 2014 (lat.)
Brommer and Møller 2011
Moreno-Rueda et al. 2012
Tingley et al. 2012
-2
-1
0
1
Effect Size
Fecundity
(c)
Mean: Latitude
Mean: Altitude
Alofs et al. 2014
Angert et al. 2011
Auer and King 2014
Betzholtz et al. 2012
Brommer 2008
Hockey et al. 2011
Pöyry et al. 2009
Sunday et al. 2015
Zuckerberg et al. 2009
Auer and King 2014
Forero-Medina et al. 2011
Freeman and Freeman 2014
Tingley et al. 2012
Zuckerberg et al. 2009
● Latitude
● Altitude
-2
-1
0
1
Effect Size
Diet Breadth
(d)
Alofs et al. 2014
Angert et al. 2011
Angert et al. 2011
Angert et al. 2011
Auer and King 2014 (alt.)
Menendez et al. 2014
Moreno-Rueda et al. 2012
Nye et al. 2009
-2
-1
0
1
Effect Size
Historic Limit
(e)
Alofs et al. 2014
Angert et al. 2011
Betzholtz et al. 2012
Hockey et al. 2011
le Roux and McGeoch 2008
Powney et al. 2014
Pöyry et al. 2009
Reif and Flousek 2012
Zuckerberg et al. 2009 (alt.)
Zuckerberg et al. 2009 (lat.)
-2
-1
0
1
Effect Size
Habitat Breadth
(f)
1
0
-1
-2
Effect Size
0
200,000
400,000
600,000
800,000
1e6
1.2e6
Study Area km^2

Figure 2: Raw and mean effect sizes for the relationship between species' traits and range shifts as a function of study-level covariates, according to the top model for each trait: (a) body size differentiating between more mobile taxa and less mobile taxa (see text for details); (b) fecundity (no covariate effects); (c) diet breadth, differentiating between studies of latitudinal versus altitudinal range shifts; (d) historic range limit (no covariate effects) (e) habitat breadth (no covariate effects); and (f) habitat breadth as a function of study area size. Error bars and orange shaded regions indicate 95% confidence intervals.

Table S1: Summary of 54 analyses relating species' traits to range shifts, including taxa studied, study location, whether the range limit investigated was latitudinal (L) or altitudinal (A), and traits tested (bold traits had significant effects on range shifts).

Study	**Taxa**	**Location**	**Range Type**	**Traits Tested**
Alofs et al. 2014	freshwater fish	Ontario, Canada	L	Fecundity, lifespan, diet breadth, body size, habitat niche, habitat breadth, harvest status, range size, historic limit
Angert et al. 2011	bird	USA	L	Migratory distance, fecundity, diet breadth, body size, wingload, flight rank, range size, historic limit
Angert et al. 2011	dragonfly	Britain	L	Migratory distance, length of flight period, fecundity, body size, flight behavior, habitat niche, range size, historic limit
Angert et al. 2011	mammal	CA, USA	A	Fecundity, lifespan, diet breadth, body size, hibernation behavior, daily rhythm, range size, historic limit
Angert et al. 2011	plant	Switzerland	A	See shed duration, flower duration, dispersal mode, disapore mass, height, habitat breadth, historic limit
Auer and King 2014	bird	USA	L, A	Migratory distance, fecundity, diet breadth, range size, historic limit
Bergamini et al. 2009	plant	Switzerland	A	Cryophily, soil acidity, soil moisture, light requirement
Betzholtz et al. 2012	butterfly	Sweden	L	Length of flight period, activity period temp., diet breadth, diet guild, body size, habitat niche
Bodin et al. 2013	plant	France	A	Growth form, light requirement
Bradshaw et al. 2014	bird	Britain	L	Body size, natal dispersal, conservation status
Breed et al. 2012	butterfly	MA, USA	L	Fecundity, diet breadth, habitat breadth, habitat niche, overwintering stage
Brommer 2008	bird	Finland	L	Migratory distance, diet guild, body size
Brommer and Møller 2010	bird	Europe, USA	L, A	Migratory distance, fecundity, diet guild, body size, habitat niche, adult survival, brain mass, thermal range, dispersal distance
Chessman 2012	invertebrate	Australia	L	Thermophily, rheophily
Comte et al. 2014	fish	France	A	Fecundity, diet niche, mobility, habitat breadth, thermophily, range size
Crimmins et al. 2011	plant	USA	A	Growth form, dispersal mode, physiognomy, fire adaptation
Davey et al. 2013	bird	Sweden	L, A	Habitat breadth, thermophily, range size
Felde et al. 2012	plant	Norway	A	Dispersal mode, cryophily, snow affinity, growth form, Ellenberg indicators

Forero-Medina et al. 2011	bird	Peru	A	Diet guild
Freeman and Freeman 2014	bird	New Guinea	A	Diet guild
Grenouillet and Comte 2014	fish	France	L	Lifespan, dispersal, thermophily, range size, historic limit
Grewe et al. 2013	dragonfly	Europe	L	Habitat niche
Grytnes et al. 2014	plant	Europe	A	Thermophily, snow preference, dispersal mode, Ellenberg indicators
Hockey et al. 2011	bird	South Africa	L	Migratory distance, diet breadth, habitat breadth
Holzinger et al.	plant	Switzerland	A	Dispersal mode, dispersal month, diaspore length
Hsieh et al. 2009	fish	Pacific	L	Thermophily, habitat niche, spawning duration
Jiménez-Alfaro et al. 2014	plant	Spain	A	Habitat breadth
Konvicka et al. 2003	butterfly	Czech Republic	A	Habitat niche, historic limit, conservation status
La Sorte and Thompson	bird	USA	L	Migratory distance
Lenoir et al. 2008	plant	Europe	A	Habitat niche
le Roux and McGeoch 2008	plant	Marion Is.	A	Habitat breadth
Lima et al. 2007	algae	Portugal Coast	-	Thermophily
Mattila et al. 2011	butterfly	Finland	L	Length of flight period, diet breadth, body size, flight behavior, habitat breadth, overwintering stage
McCain and King 2014	mammal	North America	L, A	Body size, hibernation behavior, daily rhythm, heterothermy, burrowing behavior, nesting behavior
McDonald et al. 2012	bird	USA	L	Migratory distance
Menéndez et al. 2014	invert	Europe	A	Historic limit
Moreno-Rueda et al. 2012	reptile	Spain	A	Fecundity, body size
Moritz et al. 2008	bird	CA, USA	A	Diet guild, body size, fecundity, lifespan, hibernation behavior, daily rhythm
Nye et al. 2009	fish	Atlantic	L, A	Historic limit

Parolo and Rossi 2007	plant	Italy	A	Dispersal mode, disaspore mass
Perry et al. 2005	marine fish	North Sea	L	Age at maturity, body size, growth rate
Ploquin et al. 2013	bee	Spain	A	Tongue length
Popy et al. 2010	bird	Italy	A	Habitat niche
Powney et al. 2014	plant	Britain	L	Thermophily, height, habitat breadth, Ellenberg values, life cycle
Pöyry et al. 2009	lepidoptera	Finland	L	Length of flight period, diet breadth, body size, flight behavior, larval host, habitat niche, habitat breadth, overwintering stage, conservation status, range size
Przeslawski et al. 2012	marine	Global	L	Mobility, dispersal potential, habitat niche, diet guild
Reif and Flousek 2012	bird	Czech Republic	A	Diet guild, habitat breadth, habitat niche, thermal range
Rowe et al. 2010	mammal	NV, USA	A	Habitat niche
Schmidtlein et al. 2013	plant	Germany	A	Habitat niche
Sunday et al. 2015	marine fish	Australia	L	Diet breadth, body size, range size
Tingley et al. 2009	bird	CA, USA	A	Migratory distance, fecundity, diet breadth, body size, territory type, home range
Wolf et al. 2016	plant	CA, USA	A	Seed size, growth form
Yemane et al. 2014	fish	Atlantic (Africa)	L, A	Body size, harvest status
Zuckerberg et al. 2009	bird	NY, USA	L, A	Migratory distance, diet guild, habitat niche

Table S2. Raw data for effect sizes of body size on range shifts.

Study	Effect Size	SE	Taxon	n	Years	Phylo	Lat	Exposure	Area	Mobility
Perry et al. 2005	-1.13	0.51	mfish	35	24	0	1	1.05	570000	0
Tingley et al. 2009	-0.48	0.23	bird	99	74	0	0	0.80	17300	0
Brommer 2008	-0.42	0.15	bird	116	7	0	1	-0.59	303900	0
Moreno-Rueda et al. 2012	-0.21	0.19	herp	30	65	0	0	0.30	504645	1
Bradshaw et al. 2014	-0.15	0.13	bird	116	27	1	1	0.10	241930	0
Sunday et al. 2015	-0.11	0.16	mfish	50	25	1	1	0.48	17500	0
Angert et al. 2011	-0.06	0.09	bird	143	29	0	1	0.63	7663942	0
Angert et al. 2011	0.01	0.01	plant	96	111	0	0	0.60	40000	1
Angert et al. 2011	0.03	0.06	mammal	28	86	0	0	1.00	6100	1
Betzholtz et al. 2012	0.04	0.06	invert	282	37	1	1	1.25	410340	1
Powney et al. 2014	0.12	0.03	plant	1075	52	1	1	0.10	241930	1
Pöyry et al. 2009	0.33	0.12	invert	48	8	1	1	0.59	303900	1
Alofs et al. 2014	0.94	0.22	fish	13	25	0	1	0.65	158654	1

Table S3: Raw data for effect sizes of fecundity on range shifts.

Study	Effect Size	SE	Taxon	n	Years	Phylo	Lat	Exposure	Area	Mobility
Alofs et al. 2014	0.36	0.12	fish	13	25	0	1	0.65	158654	1
Angert et al. 2011	-0.02	0.04	invert	37	40	1	1	0.25	243610	1
Angert et al. 2011	0.00	0.01	bird	143	29	1	1	0.63	7663942	0
Angert et al. 2011	0.02	0.04	mammal	28	86	1	0	1.00	6100	1
Auer and King 2014 (alt.)	0.30	0.13	bird	40	35	0	0	0.66	3099617	0
Auer and King 2014 (lat.)	-0.33	0.11	bird	40	35	0	1	0.66	3099617	0
Brommer and Møller 2011	0.26	0.17	bird	116	7	0	1	-0.59	303900	0
Moreno-Rueda et al. 2012	0.09	0.19	herp	30	65	0	0	0.30	504645	1
Tingley et al. 2009	-0.11	0.04	bird	99	74	0	0	0.80	17300	0

Table S4: Raw data for effect sizes of diet breadth on range shifts.

Study	Effect Size	SE	Taxon	n	Years	Phylo	Lat	Exposure	Area	Mobility
Zuckerberg et al. 2009 (elev.)	-0.56	0.36	bird	41	20	0	0	1.00	125384	0
Forero-Medina et al. 2011	-0.45	0.31	bird	55	41	0	0	0.79	32	0
Auer and King 2014 (elev.)	-0.31	0.13	bird	40	35	1	0	0.66	3099617	0
Tingley et al. 2009	-0.23	0.42	bird	99	74	0	0	0.80	17300	0
Freeman and Freeman 2014	0.24	0.23	bird	160	44	0	0	0.43	12	0
Auer and King 2014 (lat.)	-0.28	0.10	bird	40	35	1	1	0.66	3099617	0
Brommer 2008	-0.22	0.39	bird	116	7	0	1	-0.59	303900	0
Zuckerberg et al. 2009 (lat.)	-0.01	0.37	bird	41	20	0	1	1.00	125384	0
Pöyry et al. 2009	0.02	0.13	invert	48	8	1	1	0.59	303900	1
Hockey et al. 2011	0.10	0.56	bird	195	20	1	1	0.27	1220920	0
Betzholtz et al. 2012	0.13	0.05	invert	282	37	1	1	1.25	410340	1
Sunday et al. 2015	0.23	0.13	mfish	50	25	1	1	0.48	17500	0
Alofs et al. 2014	0.24	0.16	fish	13	25	0	1	0.65	158654	1
Angert et al. 2011	0.32	0.13	bird	143	29	1	1	0.63	7663942	0

Table S5: Raw data for effect sizes of habitat breadth on range shifts.

Study	Effect Size	SE	Taxon	n	Years	Phylo	Lat	Exposure	Area	Mobility
Zuckerberg et al. 2009 (elev.)	-0.72	0.43	bird	41	20	0	0	1.00	125384	0
Zuckerberg et al. 2009 (lat.)	-0.46	0.44	bird	41	20	0	1	1.00	125384	0
Reif and Flousek 2012	-0.08	0.06	bird	51	10	1	0	1.50	900	0
Angert et al. 2011	-0.08	0.13	plant	96	111	1	0	0.60	40000	1
Alofs et al. 2014	-0.04	0.09	fish	13	25	0	1	0.65	158654	1
Powney et al. 2014	0.14	0.04	plant	1075	52	1	1	0.10	241930	1
Pöyry et al. 2009	0.17	0.19	invert	48	8	1	1	0.59	303900	1
Betzholtz et al. 2012	0.25	0.12	invert	282	37	1	1	1.25	410340	1
le Roux and McGeoch 2008	0.42	0.45	plant	21	40	0	0	1.20	290	1
Hockey et al. 2011	0.61	0.22	bird	195	20	1	1	0.27	1220920	0

Table S6: Raw data for effect sizes of historic range limit on range shifts.

Study	Effect Size	SE	Taxon	n	Years	Phylo	Lat	Exposure	Area	Mobility
Menendez et al. 2014	-0.92	0.39	invert	30	14	0	0	0.80	2150	1
Nye et al. 2009	-0.76	0.47	mfish	36	39	0	1	1.00	265244	0
Moreno-Rueda et al. 2012	-0.47	-0.21	herp	30	65	0	0	0.30	504645	1
Auer and King 2014 (elev.)	-0.46	0.09	bird	40	35	0	0	0.66	3099617	0
Angert et al. 2011	-0.43	0.19	mammal	28	86	0	0	1.00	6100	1
Alofs et al. 2014	-0.20	0.08	fish	13	25	0	1	0.65	158654	1
Angert et al. 2011	-0.11	0.16	plant	96	111	0	0	0.60	40000	1
Angert et al. 2011	0.00	0.08	bird	143	29	0	1	0.63	7663942	0

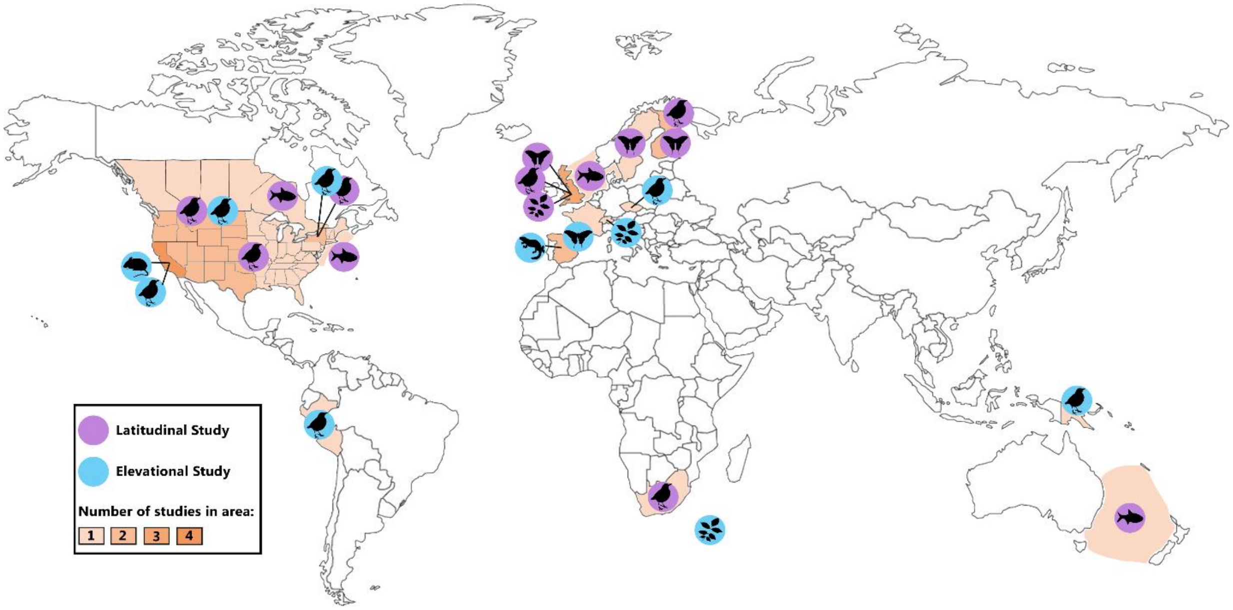

Figure S1: Map of all studies included in the meta-analysis, indicating coverage area (shaded regions), taxa (point icons), and type of range shift (point color) for each study.

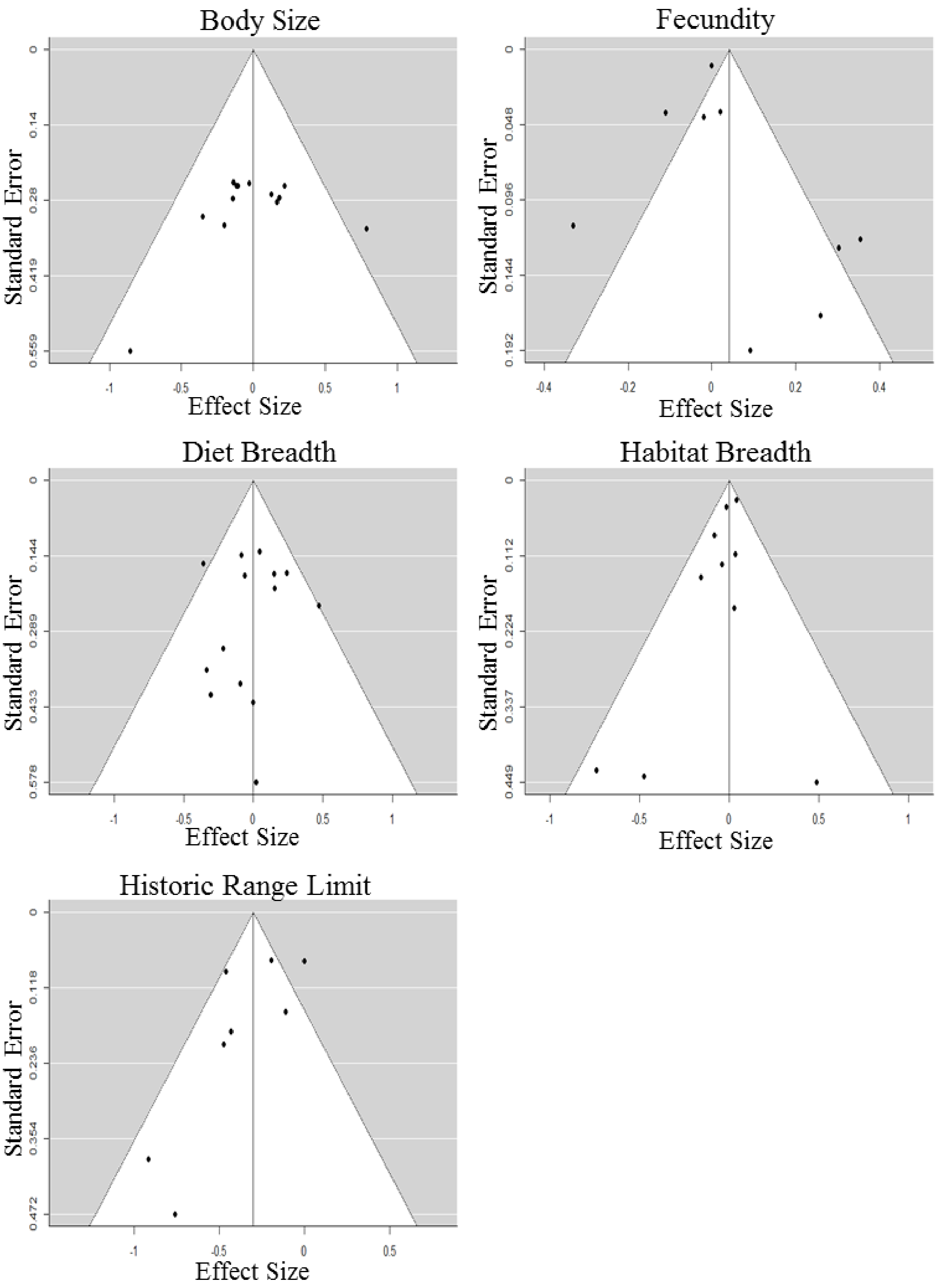

Figure S2: Funnel plots of the top model for each trait.

Figure S3: Comparison of study-level average range shifts reported in studies included in our meta-analysis, compared to studies excluded from the meta-analysis due to lack of trait data.

Appendix 1: Code used to conduct meta-analysis in R.

```
###Load metaphor package###
require(metafor)

###Read Data####
size = read.csv("body.size.csv")
diet = read.csv("diet.breadth.csv")
habitat = read.csv("habitat.breadth.csv")
fecundity = read.csv("fecundity.csv")
limit = read.csv("historic.range.limit.csv")

covs = c("null","exposure","n","phylogeny","lat.alt","area","duration","mobility")


####Body Size Analysis####
size.n = rma(effect.size,sei=se,data=size,method="PM")
size.1 = rma(effect.size, sei=se,mods=~exposure,data=size,method="PM")
size.2 = rma(effect.size, sei=se,mods=~n,data=size,method="PM")
size.3 = rma(effect.size, sei=se,mods=~phylogeny,data=size,method="PM")
size.4 = rma(effect.size, sei=se,mods=~lat,data=size,method="PM")
size.5 = rma(effect.size, sei=se,mods=~area,data=size,method="PM")
size.6 = rma(effect.size, sei=se,mods=~years,data=size,method="PM")
size.7 = rma(effect.size, sei=se,mods=~mobility,data=size,method="PM")

size.n.aic = size.n$fit.stats[5,1]
size.1.aic = size.1$fit.stats[5,1]
size.2.aic = size.2$fit.stats[5,1]
size.3.aic = size.3$fit.stats[5,1]
size.4.aic = size.4$fit.stats[5,1]
size.5.aic = size.5$fit.stats[5,1]
size.6.aic = size.6$fit.stats[5,1]
size.7.aic = size.7$fit.stats[5,1]

size.AIC = data.frame(Model = covs, AICc =
c(size.n.aic,size.1.aic,size.2.aic,size.3.aic,size.4.aic,size.5.aic,size.6.aic,size.7.aic))


####Diet Breadth Analysis####
diet.n = rma(effect.size,sei=se,data=diet,method="PM")
diet.1 = rma(effect.size, sei=se,mods=~exposure,data=diet,method="PM")
diet.2 = rma(effect.size, sei=se,mods=~n,data=diet,method="PM")
diet.3 = rma(effect.size, sei=se,mods=~phylogeny,data=diet,method="PM")
diet.4 = rma(effect.size, sei=se,mods=~lat,data=diet,method="PM")
diet.5 = rma(effect.size, sei=se,mods=~area,data=diet,method="PM")
diet.6 = rma(effect.size, sei=se,mods=~years,data=diet,method="PM")
```

```
diet.7 = rma(effect.size, sei=se,mods=~mobility,data=diet,method="PM")

diet.n.aic = diet.n$fit.stats[5,1]
diet.1.aic = diet.1$fit.stats[5,1]
diet.2.aic = diet.2$fit.stats[5,1]
diet.3.aic = diet.3$fit.stats[5,1]
diet.4.aic = diet.4$fit.stats[5,1]
diet.5.aic = diet.5$fit.stats[5,1]
diet.6.aic = diet.6$fit.stats[5,1]
diet.7.aic = diet.7$fit.stats[5,1]

diet.AIC = data.frame(Model = covs, AICc =
c(diet.n.aic,diet.1.aic,diet.2.aic,diet.3.aic,diet.4.aic,diet.5.aic,diet.6.aic,diet.7.aic))


#### Habitat Breadth Analysis####
habitat.n = rma(effect.size,sei=se,data=habitat,method="PM")
habitat.1 = rma(effect.size, sei=se,mods=~exposure,data=habitat,method="PM")
habitat.2 = rma(effect.size, sei=se,mods=~n,data=habitat,method="PM")
habitat.3 = rma(effect.size, sei=se,mods=~phylogeny,data=habitat,method="PM")
habitat.4 = rma(effect.size, sei=se,mods=~lat,data=habitat,method="PM")
habitat.5 = rma(effect.size, sei=se,mods=~area,data=habitat,method="PM")
habitat.6 = rma(effect.size, sei=se,mods=~years,data=habitat,method="PM")
habitat.7 = rma(effect.size, sei=se,mods=~mobility,data=habitat,method="PM")

habitat.n.aic = habitat.n$fit.stats[5,1]
habitat.1.aic = habitat.1$fit.stats[5,1]
habitat.2.aic = habitat.2$fit.stats[5,1]
habitat.3.aic = habitat.3$fit.stats[5,1]
habitat.4.aic = habitat.4$fit.stats[5,1]
habitat.5.aic = habitat.5$fit.stats[5,1]
habitat.6.aic = habitat.6$fit.stats[5,1]
habitat.7.aic = habitat.7$fit.stats[5,1]

habitat.AIC = data.frame(Model = covs, AICc =
c(habitat.n.aic,habitat.1.aic,habitat.2.aic,habitat.3.aic,habitat.4.aic,habitat.5.aic,habitat.6.aic,habitat.7.aic))


##Fecundity Analysis####
fecundity.n = rma(effect.size,sei=se,data=fecundity,method="PM")
fecundity.1 = rma(effect.size, sei=se,mods=~exposure,data=fecundity,method="PM")
fecundity.2 = rma(effect.size, sei=se,mods=~n,data=fecundity,method="PM")
fecundity.3 = rma(effect.size, sei=se,mods=~phylogeny,data=fecundity,method="PM")
fecundity.4 = rma(effect.size, sei=se,mods=~lat,data=fecundity,method="PM")
fecundity.5 = rma(effect.size, sei=se,mods=~area,data=fecundity,method="PM")
```

```
fecundity.6 = rma(effect.size, sei=se,mods=~years,data=fecundity,method="PM")
fecundity.7 = rma(effect.size, sei=se,mods=~mobility,data=fecundity,method="PM")

fecundity.n.aic = fecundity.n$fit.stats[5,1]
fecundity.1.aic = fecundity.1$fit.stats[5,1]
fecundity.2.aic = fecundity.2$fit.stats[5,1]
fecundity.3.aic = fecundity.3$fit.stats[5,1]
fecundity.4.aic = fecundity.4$fit.stats[5,1]
fecundity.5.aic = fecundity.5$fit.stats[5,1]
fecundity.6.aic = fecundity.6$fit.stats[5,1]
fecundity.7.aic = fecundity.7$fit.stats[5,1]

fecundity.AIC = data.frame(Model = covs, AICc =
c(fecundity.n.aic,fecundity.1.aic,fecundity.2.aic,fecundity.3.aic,fecundity.4.aic,fecundity.5.aic,fe
cundity.6.aic,fecundity.7.aic))


####Historic limit Analysis####
limit.n = rma(effect.size,sei=se,data=limit,method="PM")
limit.1 = rma(effect.size, sei=se,mods=~exposure,data=limit,method="PM")
limit.2 = rma(effect.size, sei=se,mods=~n,data=limit,method="PM")
limit.3 = rma(effect.size, sei=se,mods=~phylogeny,data=limit,method="PM")
limit.4 = rma(effect.size, sei=se,mods=~lat,data=limit,method="PM")
limit.5 = rma(effect.size, sei=se,mods=~area,data=limit,method="PM")
limit.6 = rma(effect.size, sei=se,mods=~years,data=limit,method="PM")
limit.7 = rma(effect.size, sei=se,mods=~mobility,data=limit,method="PM")

limit.n.aic = limit.n$fit.stats[5,1]
limit.1.aic = limit.1$fit.stats[5,1]
limit.2.aic = limit.2$fit.stats[5,1]
limit.3.aic = limit.3$fit.stats[5,1]
limit.4.aic = limit.4$fit.stats[5,1]
limit.5.aic = limit.5$fit.stats[5,1]
limit.6.aic = limit.6$fit.stats[5,1]
limit.7.aic = limit.7$fit.stats[5,1]

limit.AIC = data.frame(Model = covs, AICc =
c(limit.n.aic,limit.1.aic,limit.2.aic,"n/a",limit.4.aic,limit.5.aic,limit.6.aic,limit.7.aic))


#### Funnel plots of top model for each trait####
funnel(size.7)
funnel(diet.4)
funnel(habitat.5)
funnel(fecundity.n)
funnel(limit.n)
```

Chapter 2.

A century of climate and land-use change cause species turnover without loss of beta diversity in California's Central Valley

Abstract

Climate and land-use change are projected to be the greatest threats to biodiversity over the coming century, but few studies have directly measured their simultaneous impacts on species distributions. We used a unique historic resource – early 19th century bird surveys conducted by Joseph Grinnell and colleagues – paired with contemporary resurveys a century later to examine changes in bird distributions in California's Central Valley, one of the most intensively modified agricultural zones in the world and a region of heterogeneous climate change. We analyzed species- and community-level occupancy using multispecies occupancy models that explicitly accounted for imperfect detection probability, and developed a novel, simulation-based method to compare the relative influences of climate and land-use covariates on site-level species richness and beta diversity (measured by Jaccard similarity). Surprisingly, we show that mean occupancy, species richness, and between-site similarity have remained remarkably stable over the past century. Stability in community-level metrics masked substantial changes in species composition; occupancy declines of some species were equally matched by increases in others, predominantly species with generalist or human-associated habitat preferences. Bird occupancy, richness, and diversity were driven most strongly by water availability (precipitation and percent water cover), indicating that both climate and land-use are important drivers of species distributions. Water availability had much stronger effects than temperature, urbanization, and agricultural cover, which are typically thought to drive biodiversity decline.

Introduction

Global climate and land-use change are projected to be the greatest threats to biodiversity over the coming century (Sala et al. 2000), with implications for community functions and ecosystem services (Cardinale et al. 2012). The effects of climate and land use on the geographic structuring of biodiversity have largely been studied independently (Thomas et al. 2004, Karp et al. 2012, Tingley and Beissinger 2013, Newbold et al. 2015, Ibáñez-Álamo et al. 2017). However, realistic scenarios must consider the simultaneous effects of these two drivers (Travis 2003, Hof et al. 2011, Parmesan et al. 2013, Ferger et al. 2017). Some studies suggest that climate is more important than land-use in determining species distributions (Thuiller et al. 2004, Sohl 2014, Bucklin et al. 2015), but the continental scale of these analyses could underestimate the importance of land use in regions of intense urban or agricultural development.

Species demonstrate heterogeneous distributional responses to both climate and land-use (McKinney 2002, Walther et al. 2002, Tingley et al. 2012, Carrara et al. 2015), although these two drivers may favor species with similar ecological traits (Frishkoff et al. 2016). Climate and land-use change are associated with decreased occupancy for a wide range of species, particularly those with low mobility or specialized habitat requirements (Tingley and Beissinger 2013, Carrillo-Rubio et al. 2014, Distler et al. 2015). At the same time, occupancy typically increases in species tolerant to altered habitats, particularly generalists (McKinney 2002, Rahel 2002, Carrara et al. 2015, MacLean and Beissinger 2017). Thus, the combined effects of climate and land-use change should cause a loss of species richness and increased homogenization at the community level (Bonebrake et al. 2016, Frishkoff et al. 2016, Karp et al. 2017). There is however, considerable debate on whether local species richness has declined globally (Newbold et al. 2015, Gonzalez et al. 2016), as some studies demonstrate a surprising lack of diversity loss despite climate or land-use change (Dornelas et al. 2014, Vellend et al. 2017).

We quantified the influence of climate and land-use on community composition by comparing early 20th century bird communities to their contemporary counterparts in the California Central Valley, a 47,000 km^2 region that has undergone intensive agricultural and urban expansion, as well as heterogeneous climate change. Since the early 1900s, the Central Valley has been converted from seasonal wetlands and alkali scrub to one of the most intensely developed agricultural regions in the world, interspersed with several large urban centers (Frayer et al. 1989, Nelson et al. 2003). Concurrently, the valley has undergone spatially heterogeneous changes in temperature and precipitation patterns (Rapacciuolo et al. 2014). We used unique historic resources – early 1900s systematic bird surveys and land use maps – paired with modern resurveys and measures of land cover and climate to quantify bird species occupancy.

We asked: (1) how have community-level occupancy, richness, and diversity changed over the past century?; (2) how has species-level occupancy changed and to what extent can these changes be explained by species' traits?; and (3) what is the relative importance of climatic and land-use covariates to occupancy, species richness, and beta diversity (as measured by Jaccard similarity) within each survey period? We predicted that more bird species would decrease than increase in occupancy, and that contemporary bird communities would contain fewer species and be more homogeneous than their historic counterparts. We also predicted that species-level changes in occupancy would be related to body mass, clutch size, habitat breadth, and diet breadth. Finally, we predicted that land-use would have a greater influence on site-level occupancy, richness, and diversity than climate, especially during the modern resurvey period due to the dominance of human-altered habitats.

Materials and Methods

Study Area

We resurveyed bird diversity in the Central Valley of California at 41 sites surveyed prior to 1925 by Joseph Grinnell and seven collaborators from the Museum of Vertebrate Zoology at UC Berkeley (Figure S1). The valley extends approximately 640 km north to south and on average 64 km across, bordered on the east by the Sierra Nevada foothills and on the west by the Coast Ranges. The natural vegetation of this ecoregion is a mosaic of riparian belts and seasonal wetlands within a flat grassland matrix, with limited coverage of oak woodland along the foothills and saltbrush scrub in the southern valley (Nelson et al. 2003).

Although localized agricultural development was well under way as early as the 1890s (Sumner et al. 2003), large scale expansion occurred after an extensive networks of canals and reservoirs were constructed as part of the Central Valley Project in the 1930s and the California State Water Project in the 1950s (Gilmer et al. 1982). By the early 2000s, the valley had lost over 90 percent of its original four million acres of wetland (Frayer et al. 1989), and approximately 70 percent of the valley was under cultivation (Sleeter 2007). This agricultural land continues to be one of the most productive regions in the United States (Sumner et al. 2003), and urban areas currently have one of the fastest population growth rates in California (U.S. Census Bureau 2010). Historic maps and descriptions suggest that habitat loss over the past century has been primarily from conversion of a natural type to urban or agriculture, or from loss/construction of waterways and reservoirs, with limited transitions among natural land cover types (Nelson et al. 2003, Sleeter 2007). Field notebooks kept by Grinnell and colleagues do not provide detailed maps of vegetation cover, but do describe the dominant natural plant communities, which have not changed qualitatively at any of our sites.

Bird surveys

Collection of historic and modern bird survey data followed established protocol for the Grinnell Resurvey Project (Tingley et al. 2009, 2012, Tingley and Beissinger 2013). Field journals kept by historic researchers provide detailed descriptions and maps of survey routes, as well as systematic lists of bird species observed each day. Historic surveys occurred between 1912 and 1923 (late March through July). Each site had an average of 3.7 consecutive days of surveys (minimum 1, maximum 11).

We conducted modern resurveys during the breeding seasons (April through July) of 2015 and 2016. At each site, we created a transect of 10 point count stops placed 250 m apart, corresponding as closely as possible to the route followed by the historic surveyors and the habitats that they visited. We recorded all birds seen or heard using variable-distance point counts lasting seven minutes. Counts began at dawn, and sites were surveyed daily over three consecutive days to allow estimation of detection probability (Dorazio et al. 2006).

We excluded species from our dataset if they were wetland or open water obligates, specifically shorebirds, pelicans, cormorants, grebes, and ducks (except the generalists mallard and Canada goose; see Table S1 for scientific names of all species). The required habitats of these species were not well sampled by our survey protocol, and detections during our surveys were typically fly-overs. We also excluded species migrating through the study area, which were identified if their breeding range on NatureServe (Natureserve 2017) did not include any part of the California Central Valley. The final dataset consisted of 110 species in the historic survey period and 107 species in the modern survey period.

Historic land cover mapping

Digital maps of historic land-use in California were not available at a suitable resolution or spatial extent, and historical map products created by the Wieslander Project (Kelly et al. 2008) or the San Francisco Estuary Institute (Whipple et al. 2012) do not include most of the Central Valley. We created maps of land cover within 1 km of our survey transects by hand-digitizing historic maps from sources discussed below using ArcMap (Figure S2). While it would have been ideal to map different natural land covers historically present in the Central Valley (i.e., grassland, wetland, scrub, riparian, and oak woodland), we were unable to find corresponding historic vegetation maps. Instead, we focused our analysis on land use categories associated with habitat conversion in the Central Valley. These land use categories were urban, agriculture, and water. We found limited evidence for shifts among natural habitat types based on site descriptions in the historic field notes, and based on the coarse-resolution historic map series developed by the Central Valley Historic Mapping Project (Nelson et al. 2003). We believe our three focal land-use change categories accurately capture the processes of habitat conversion most relevant to changes in bird occupancy.

Cover of water and urban area were mapped using historic USGS topographic maps (c.1906-1932). Water bodies were outlined directly as polygons. Urban area was mapped as buildings (area of the building icon on the topographic map plus a buffer of 50m) and roads (digitized as line features from the topographic map, then given a width of 30m). Area of historic agriculture was delineated using a series of three maps of irrigated land in the state of California published by the U.S. Department of Agriculture (USDA 1922). We converted our digitized historic land cover from vector format to raster format at 30m resolution per pixel, corresponding to the National Land Cover Database used for contemporary sites (Jin et al. 2013).

Multispecies occupancy model

Multispecies occupancy models use a hierarchical framework to produce estimates of species' occupancy while accounting for heterogeneity in detection probability (Dorazio and Royle 2005, Iknayan et al. 2014). We modeled historic and resurveyed sites separately using two single-season occupancy models (MacKenzie et al. 2002, Tingley and Beissinger 2009). This approach is useful when survey periods are separated by sufficient time to satisfy the assumption of independence (Moritz et al. 2008, Tingley and Beissinger 2009, Iknayan et al. 2014), and when colonization and extinction parameters in a multi-season model have difficulty converging due to data limitations (MacKenzie et al. 2003).

Probabilities of occupancy and detection were modelled as linear combinations of site- and survey-level covariates. Following previous models of birds in California (Tingley and Beissinger 2013), detection probability was modeled as a function of season, defined as the Julian day (jday = 1 on 1 January). Probability of detection for the i-th species at the j-th site on the k-th visit was modelled as follows:

$$\mathrm{logit}(p_{i,j,k}) = \alpha_{0,i} + \alpha_{1,i}\mathrm{jday}_{j,k}$$

where $\alpha_{0,i}$ and $\alpha_{1,i}$ are coefficients for detectability for species i.

Occupancy was modeled as a linear function of site-level maximum second-quarter temperature (temp) and mean second-quarter precipitation (precip; quarterly climate variables were chosen to correspond to the breeding season and showed similar trends to annual climate data), percent cover of water (water), percent cover of built-up area (urban), and percent cover of agriculture (ag). In a multispecies occupancy model, the effects of covariates on individual species occupancy are allowed to vary, as should be expected due to differences in behavior and life history, but species-specific effects are assumed to come from a common community-level hyperdistribution (Iknayan et al. 2014). Occupancy was modeled as follows, where $\beta_{0,i}, \ldots, {}_{5,i}$ are species-specific model coefficients for occupancy:

$$\text{logit}(\psi_{i,j}) = \beta_{0,i} + \beta_{1,i}\text{temp}_j + \beta_{2,i}\text{precip}_j + \beta_{3,i}\text{water}_j + \beta_{4,i}\text{urban}_j + \beta_{5,i}\text{ag}_j\ .$$

Covariates were centered at 0 and normalized to a standard deviation of 1 prior to analysis. Climate covariates (temperature and precipitation) were obtained from 800m resolution interpolated maps produced by the PRISM climate group (Daly et al. 2002), and averaged over 30-year periods corresponding to the historic (1900-1929) and modern (1987-2016) surveys. Land cover covariates were calculated for a 200m buffer around the modern survey transects. Buffers were based on the modern survey transects because they were more precisely defined spatially, while still corresponding to the same area described verbally for the historic surveys. A 200m buffer was chosen corresponding to the maximum distance at which bird species could be detected during the modern surveys. Modern land cover data was obtained from the National Land Cover Database (Jin et al. 2013). Historic land cover data was obtained from the hand digitized maps described above.

We specified two community-level measures in the model that were direct functions of estimated parameters. They were calculated from posterior draws of the Markov Chain Monte Carlo runs. Species richness at the j-th site, N_j, was calculated as

$$N_{\text{j}} = \sum_{i=1}^{n} z_{i,j}$$

where $z_{i,j}$ is the model-estimated matrix of true occurrence for each species at a site (0 or 1; for a more detailed description of $z_{i,j}$ and its calculation, see Dorazio and Royle 2005) and n is the total number of potential species within each survey period ($n_{modern} = 107$, $n_{historic} = 110$).

Similarity in species composition between two sites was calculated using the Jaccard Index (Real and Vargas 1996). Within each survey period, we estimated Jaccard similarity, J, between two sites as

$$J_{a,b} = \frac{\sum_{i=1}^{n} z_{i,a} z_{i,b}}{N_a + N_b - \sum_{i=1}^{n} z_{i,a} z_{i,b}}$$

for sites $a = 1, 2, \ldots, 41$ and $b = 1, 2, \ldots, 41$, where n is the total number of potential species within each survey period. This yielded a total of 820 unique site pairs for each survey period.

Bayesian parameter estimation was run with WinBUGS (Lunn et al. 2000) via R using the package “R2WinBUGS” (Sturtz et al. 2005). We used uninformative priors for the means and variances of the hyper-parameters. The full model code is provided in Appendix 1 We ran three parallel chains of length 50000, discarding the first 40000 as burn-in, and used a thinning rate of 10. This resulted in a posterior distribution consisting of 3000 samples for each parameter. Convergence was assessed by visual inspection of traceplots and by using the

Gelman-Rubin convergence diagnostic (Gelman and Hill 2007), with all diagnostic values <1.1. Adequacy of the model was assessed using Bayesian p-values (Gelman et al. 1996, Zipkin et al. 2009). Values closer to 0 or 1 indicate that the model was inadequate. For our dataset Bayesian p-values were estimated as 0.49 for the historic surveys and 0.47 for the modern surveys, indicating that our models provided adequate description of the data.

Species' traits

Species' functional and life history traits mediate sensitivity and ability to move in response to climate and land-use change (Buckley & Kingsolver, 2012; Estrada *et al.*, 2016), and may therefore explain heterogeneity in observed distributional changes (Angert et al. 2011, Auer and King 2014), though a recent meta-analysis revealed that, of several frequently analyzed traits, only habitat breadth has been a consistent predictor of range shifts (MacLean and Beissinger 2017).We tested whether traits explained variation in species-specific change in mean occupancy between the historic and modern survey period. Body size (mean adult mass) and clutch size (average per female) data were obtained from the online Encyclopedia of Life (Parr et al. 2014). Diet breath (number of food types consumed) was obtain from Elton Traits (Wilman et al. 2014). Habitat preference was obtained from The Birds of North America Online (Rodewald 2015), and simplified to a binary variable separating species with specialized natural habitat preferences from those with generalist or human-adapted habitat preferences (i.e. foraging and/or nesting commonly in manmade structures or habitats). We used linear mixed models to analyze change in species occupancy as a function of traits, with species as a random effect. To incorporate uncertainty from our occupancy model, we weighted the mean change in occupancy for each species by the corresponding inverse variance in occupancy change, so that species with smaller variance in occupancy change were given more weight. The full model set consisted of all single trait models (*n*=4) and all combinations of two traits (*n*=6), which were compared using AIC_c.

Covariate effects on community similarity and species richness

The effects of covariates on species richness and similarity were not directly estimated within the occupancy model, so we developed a method to approximate these effects using posterior distributions from the model output. Both species richness and Jaccard similarity are functions of the occupancy states, $z_{i,j}$, but these occupancy states were random variables in the model, with probabilities that depended on covariates. Therefore, we calculated expected species richness and expected Jaccard similarity based on the model's predicted probabilities of occupancy. The expected values are averages over every species' occupancy status in every site for species richness, or in each of two sites for Jaccard similarity. We then calculated the partial derivatives of expected species richness and similarity with respect to each of the covariates ($dE[J_{j1,j2}]/dcov$ and $dE[N_j]/dcov$ respectively), where *cov* refers to temperature, precipitation, water, urban, or agriculture. A larger derivative (i.e. a steeper slope) indicated a covariate had greater relative influence on expected richness or similarity, relative to other covariates.

For species richness, the expected richness at a hypothetical site j, $E[N_j]$, was related to the species-specific coefficients as follows:

$$E[N_j] = \sum_{i=1}^{n} expit(\beta_{0,i} + \beta_{1,i}\mathrm{temp}_j + \beta_{2,i}\mathrm{precip}_j + \beta_{3,i}\mathrm{water}_j + \beta_{4,i}\mathrm{urban}_j + \beta_{5,i}\mathrm{ag}_j)$$

where $\beta_{0,i}, \ldots, {}_{5,i}$ are species-specific coefficients estimated by the occupancy model. We calculated $dE[N_j]/dcov$ from this function directly using the grad() function from the “numDeriv” package.

While the expected species richness can be calculated analytically, this cannot be done for expected Jaccard similarity. This is because the expected Jaccard similarity is a summation of a non-linear function of occupancy status over all possible values of occupancy status at each pair of sites. Since the occupancy status for a site includes the occupancy of each species, the expected value is a very high dimensional summation, so we implemented the calculation and its derivative using Monte Carlo methods. The goal of this approach was to simulate the relationship between expected Jaccard similarity and each covariate (while holding all other covariates constant at their mean value), and then calculate the derivatives of the resulting curves.

Since Jaccard similarity is calculated between pairs of sites, we considered how similarity changed as a covariate value varied at one site, while the second site was held constant at a reference value (i.e., the mean standardized covariate value of 0). We began by calculating occupancy probability at the reference site for each species. For each occupancy probability, we then simulated 1000 vectors of occupancy (0 or 1 for each species).

For each covariate being tested, we calculated the occupancy probability for each species across the full range of the covariate’s observed (standardized) values at our survey sites, using intervals of 0.05, and setting other covariates to their mean standardized value of 0. For each covariate value, we then simulated 1000 vectors of occupancy for each species. We calculated Jaccard similarity between the 1000 vectors of occupancy for each test covariate value and the 1000 vectors of occupancy for the reference site, resulting in 1000 values of simulated Jaccard similarity for each value across the covariate’s range.

We then used the simulated Jaccard similarity values to estimate the derivative of expected Jaccard similarity with respect to the covariate. We did this by fitting a smooth function, for which we chose simply a cubic function since it was adequate to the task. We fit one cubic regression across all the simulated Jaccard values as a function of the covariate, using the lm() function in R. We then calculated the derivative of this function at the mean covariate value (i.e. 0) using the grad() function from the “numDeriv” package in R. To account for uncertainty in our occupancy model output, we repeated this entire process across all 3000 posterior values.

We also calculated the partial derivatives of richness with respect to each of the covariates using the Monte Carlo method described for Jaccard similarity. We did this to verify that the Monte Carlo results would match the analytic results, and to provide assurance that the Monte Carlo calculations for Jaccard were correct. The partial derivatives of richness with respect to each covariate were similar, regardless of whether they were calculated analytically or with our Monte Carlo method. We present results for species richness based on the Monte Carlo method to maximize comparability with results for Jaccard similarity.

Results

Climate and land use change over the past century in the Central Valley

Sites experienced heterogeneous changes in climate and land use over the past century (Figure S3). Across all sites, the maximum second quarter temperature decreased slightly by an average ± 1SE of 0.26 ± 0.10 °C (range = -2.31 – 1.14), mean second quarter precipitation increased by 0.64 ± 0.14 cm (range = -0.85 – 3.85), water cover decreased by 2.54 ± 0.89% (range = -25 – 10%), urban cover increased by 15.03 ± 2.08% (range = -4 – 55%), and agricultural cover increased by 12.42 ± 4.83% (range = -67 – 78%).

Species-level changes in occupancy

Bird species varied greatly in their responses to climate and land-use change in the Central Valley. Of the 122 species analyzed, 27 significantly decreased in occupancy, 35 increased in occupancy, and 60 showed no significant change (Figure 1 and Table S1). Because the distribution of species increasing and decreasing was roughly equal, there was no overall change in mean occupancy across all species (mean ± 1SE = 0.01 ± 0.02).

Changes in occupancy for individual species were highly heterogeneous (Figure 1 and Table S1). Species with the largest significant increases in occupancy (greater than 33%) were predominantly exotics and human adapters, including Eurasian collared-dove, brown-headed cowbird, European starling, northern mockingbird, Anna’s hummingbird, great egret, common raven, rock pigeon, and mourning dove. Species with the largest significant decreases in occupancy (greater than 33%) were the American kestrel, western meadowlark, burrowing owl, American goldfinch, loggerhead shrike, chipping sparrow, Bell’s sparrow, turkey vulture, and northern flicker. Fifteen species disappeared from our study sites over the past century; nine of the species had low (<0.15) historic occupancy (mountain bluebird, bank swallow, Hammond’s flycatcher, black-chinned sparrow, Allen’s hummingbird, Le Conte’s thrasher, Costa’s hummingbird, Lewis’ woodpecker, and purple martin), but six of the species were relatively common (>0.20 occupancy) historically (Bell’s vireo, Brewer’s sparrow, burrowing owl, hairy woodpecker, hermit thrush, and ruby-crowned kinglet). Of the twelve species new to the modern survey period, six were rare (occupancy <0.15) colonizers from neighboring ecoregions on the edges of the Central Valley (brown creeper, pileated woodpecker, white-tailed kite, common ground dove, Steller’s jay, osprey), two were exotic species occurring at low occupancy (ring-necked pheasant and rose-ringed parakeet), and four were well-known expanders in California including three exotic (Eurasian collared-dove, rock pigeon, wild turkey) and one native (great-tailed grackle) species.

Species-level changes in occupancy were likely driven by habitat preferences. Habitat preference explained the greatest amount of variation in occupancy change (AIC_c weight = 0.31

for single-covariate model; AIC_c weight = 1.00 for all models including habitat) compared to body size, diet breadth, clutch size, or the null model (Table 1).

Habitat generalists and species that utilize human-modified habitats were more likely to increase in occupancy than were species using other types of habitat, which tended to remain stable in occupancy (Figure 2).

Avian community change

Both species richness per site and Jaccard similarity between sites changed little on average over the past century (Figure 3). Richness increased slightly by 1.91 species per site on average (95% credible interval = -14.17 – 17.76; Figure 3a). Jaccard similarity between sites (which ranges from 0 to 1) also increased slightly by 0.06 on average (95% CI = -0.11 – 0.23; Figure 3b).

Community-level occupancy was driven primarily by precipitation and water cover in both the historic and modern periods (Figure 4a). Precipitation had the greatest mean effect across all species-level coefficients followed closely by the percent cover of water; both effects were positive. Temperature had a strong negative effect on occupancy in the modern survey period, but had a minimal effect during the historic survey period. Urban and agricultural land use had no significant community-level effects on occupancy during either survey period. We found the same pattern for covariate effects on the derivatives of expected species richness (Figure 4b) and Jaccard similarity (Figure 4c).

Discussion

Over the past century, birds of the Central Valley responded heterogeneously to climate and land-use change. Occupancy increased for predominantly generalist and exotic species, while species sensitive to human habitat modifications declined (Figure 2). Nevertheless, species-level changes were surprisingly well balanced, resulting in unexpected stability in community richness and beta diversity (Figure 3). Occupancy, richness, and diversity were determined in both survey periods predominantly by water availability – precipitation and the percent cover of surface water (Figure 4) – suggesting that the dichotomy between climate and land-use as drivers of biodiversity may be an oversimplification.

Bird species change driven by habitat preference

Despite large changes in climate and land use in California’s Central Valley, the majority of species exhibited stable or increasing occupancy over the past century (Figure 1). Unsurprisingly, occupancy increased the most for exotic species that have become well-established in California since the historic surveys, including the Eurasian collared-dove, European starling, and rock pigeon. Another top expander, the wild turkey, was purposefully introduced to California by the Department of Fish and Game several times throughout the 1900s (Gardner et al. 2004). However, we also found large increases in occupancy by several native North American bird species that are known to favor human-modified habitats, including Anna’s hummingbird (Greig et al. 2017), common raven (Kristan and Boarman 2007), brown-headed cowbird (Rothstein et al. 1980), and great-tailed grackle (Wehtje 2003). Overall, increases in occupancy predominantly occurred in species that were habitat generalists or human adapters (Figure 2).

Large decreases in occupancy occurred for several bird species with well-documented population declines within and beyond California, including the American kestrel (Smallwood et al. 2009) and burrowing owl (Klute et al. 2003). Other top decliners were predominantly species with relatively specialized habitat preferences, including scrub-specialists like the California thrasher, wetland specialists such as the common yellowthroat, and open habitat specialists such as loggerhead shrike, turkey vulture, lark sparrow, and western meadowlark. Species that were fairly common during the historic survey period but completely or nearly absent during modern surveys included the state endangered Bell's vireo and several Species of Special Concern such as the yellow-breasted chat (California Department of Fish and Wildlife 2017). The yellow-billed magpie, one of California's two endemic bird species, showed no change in occupancy, though the extremely low probability of occupancy in both survey periods (~0.02) should be taken into account before comparing this result to apparent population declines documented by other studies (Crosbie et al. 2014).

Community stability and the absence of biotic homogenization in response to a century of climate and land-use change

At the community-level, we found no significant change in average occupancy (Figure 1) or in species richness per site (Figure 3a). This result strongly contradicts with expectations that occupancy and richness should decrease at sites experiencing substantial anthropogenic land-use and climate change (McKinney 2002, Wiens et al. 2009, Distler et al. 2015, Newbold et al. 2015). We were also surprised to find a greater proportion of species increasing in occupancy by >0.1 in the Central Valley (31%) compared to similar resurvey efforts in far less modified regions of the California Sierra Nevada (15%; Tingley *et al.*, 2012), Mojave desert (2%; Iknayan et al., unpublished data), and Coast Ranges (13%; P.N. Epanchin and S.R. Beissinger, unpublished data). The Central Valley also had proportionally fewer species decreasing by >0.1 (29%) than the Mojave Desert (39%) or Coast Ranges (33%). This counterintuitive pattern of stable or increased site-level species richness has been documented elsewhere (Sax and Gaines 2003, Dornelas et al. 2014), but is unusual for a study region like ours that has undergone dramatic increases in urbanization, agriculture, and climate during the century between our surveys (Cardinale 2011, Karp et al. 2011, 2017, Frishkoff et al. 2016).

Despite the increasing prevalence of generalists and human adapters in the Central Valley since Grinnell conducted surveys, Jaccard similarity changed little between the historic and modern survey periods (Figure 3b). This result contradicts the expectation that climate and land-use change should result in biotic homogenization over time (McKinney 2002, Karp et al. 2012, Bonebrake et al. 2016, Frishkoff et al. 2016, Ibáñez-Álamo et al. 2017). It is encouraging that avian diversity has persisted over the past century in one of the most heavily modified landscapes on the planet (Galloway and Riley 1999). We suspect that bird communities are being maintained by the stark contrast between the agricultural matrix and preserved riparian corridors (McKinney et al. 2011), and by human landscape modifications that increase food, such as feeding stations and irrigated landscaping (Beissinger and Osborne 1982, Marzluff et al. 2001) in an otherwise arid region. Further research is needed to explore these relationships.

Species richness at a site may be stable or even increase when generalist and invasive species replace more sensitive species (Prendergast et al. 1993, Kerr 1997, McKinney 2002). This occurred in the Central Valley over the past century, given the results of our trait analysis (Figure 2) and the identities of our top increasing species (Figure 1b). However, the lack of biotic homogenization in our study is a puzzling result, although it could be related to our choice of diversity metric. While species diversity is a hallmark metric of conservation (Ibáñez-Álamo et al. 2017), recent studies have revealed important effects of land-use change on functional and phylogenetic diversity (Karp et al. 2011, Frishkoff et al. 2014, Sol et al. 2017), and these metrics deserve consideration in future work. Nevertheless, climate change is expected to produce non-analog communities throughout California and elsewhere (Williams and Jackson 2007, Stralberg et al. 2009), which could act to counter biotic homogenization.

Water availability drives occupancy in the Central Valley

Community-level occupancy, richness, and similarity were driven primarily by water availability – precipitation and the percent cover of surface water in the vicinity of the survey sites – in both centuries that we surveyed (Figure 4). We were surprised by the low importance of urban and agricultural cover in structuring avian communities, given the large extent of land-use change in our study area and the strong influence of human habitat association on species-level occupancy changes.

Water availability represents a combination of climate and land-use impacts that affect avian occupancy in the Central Valley, challenging previous findings that climate alone is the primary determinant of bird distributions (Thuiller et al. 2004, Sohl 2014, Bucklin et al. 2015). Precipitation had the largest influence on avian occupancy in the arid environment of the Central Valley, while temperature had a small influence in the modern survey period (Figure 4). We found little effect on occupancy of the two most commonly analyzed drivers of land use, urban and agricultural cover. However, water cover – an anthropogenic land-use driver influenced by highly-managed canals and reservoirs in the Central Valley – had an influence similar to precipitation. Since the early 1900s, the Central Valley has lost over 1.9 million acres of wetland and gained at least 3.3 million acres of agricultural and urban land (Nelson et al. 2003). This region is naturally hot and arid, and biodiversity was historically associated with riparian corridors and seasonal wetlands (Frayer et al. 1989, Nelson et al. 2003). The link between water and bird communities has persisted despite massive anthropogenic landscape alterations.

Our finding that precipitation and secondarily temperature are more influential to community-level metrics than the extensive agriculture and urban cover in the Central Valley provides powerful evidence for the severe threat posed to future biodiversity by climate change and drought. At the same time, anthropogenic habitat modification clearly plays an important role in bird communities of the Central Valley, given the influence of water cover to occupancy, as well as the importance of generalist tendencies and human habitat tolerance to species' level occupancy change. Addition of water to this arid landscape may create anthropogenic refugia that ameliorate the effects of climate change (Morelli et al. 2012, 2016). It will be important to continue to study the combined effects of these drivers on species distributions to better understand how their influence may vary by scale and geographic context.

Acknowledgements

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Table 1: AICc rankings for linear mixed effects models of traits as predictors of occupancy change, weighted by variance in occupancy change.

Model	k	AICc	ΔAICc	AICc Weight	Log Likelihood
Habitat	4	-38.95	0.00	0.31	23.64
Habitat + Diet	5	-38.93	0.02	0.31	24.72
Habitat + Size	5	-38.76	0.19	0.28	24.64
Habitat + Clutch	5	-36.79	2.15	0.11	23.66
Diet	4	13.43	52.38	0.00	-2.55
Diet + Size	5	14.30	53.25	0.00	-1.89
Diet + Clutch	5	15.60	54.55	0.00	-2.54
Size	4	17.06	56.01	0.00	-4.36
Null	3	17.22	56.17	0.00	-5.51
Clutch	4	19.19	58.14	0.00	-5.43
Size + Clutch	5	19.24	58.19	0.00	-4.36

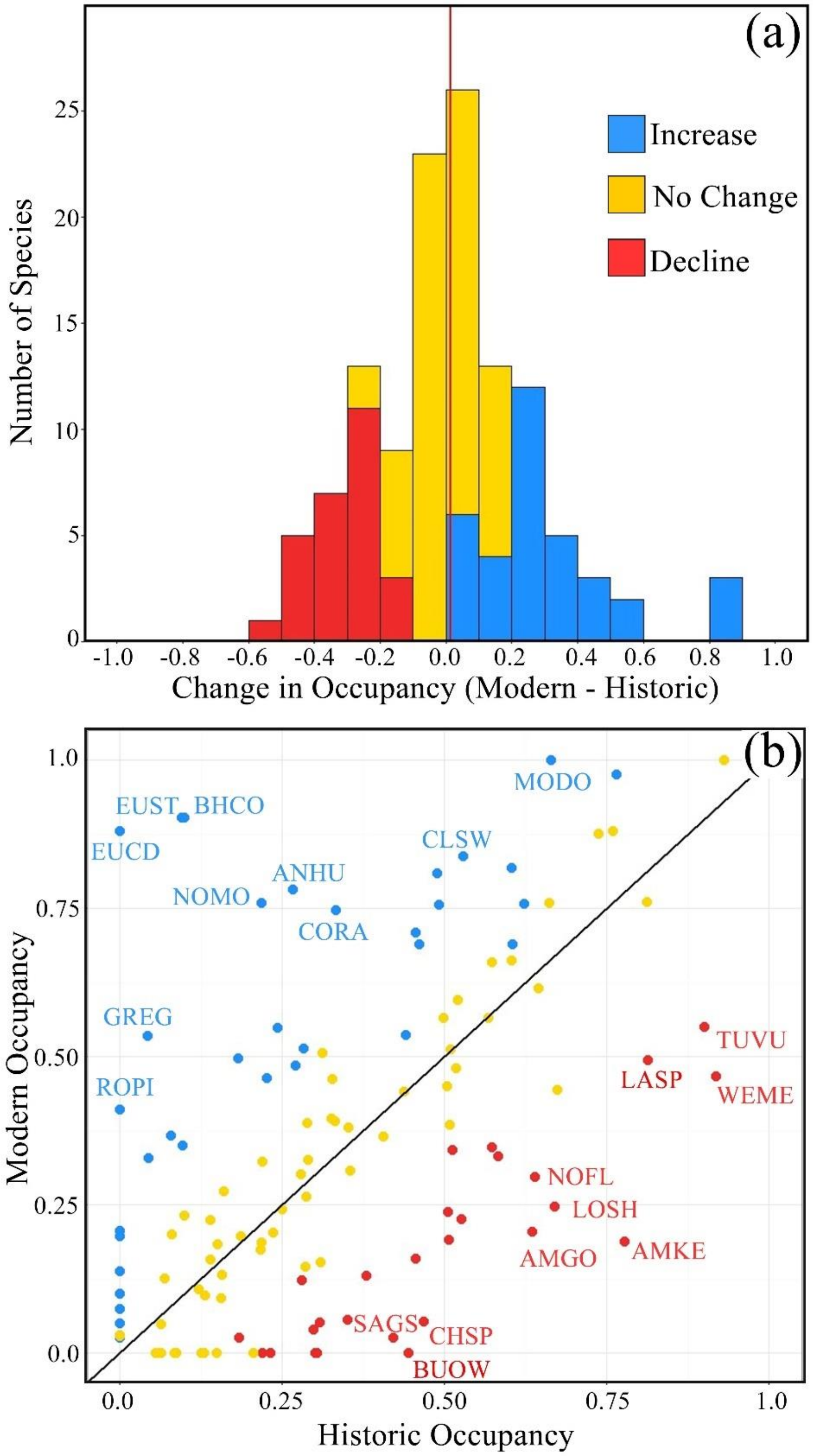


Figure 1: (a) Change in the proportion of sites occupied between historic (1912-1923) and modern (2015-2016) survey periods for bird species of the Central Valley, with colors indicating significant increases, decreases, or no change; (b) Comparison of historic and modern occupancy for all species, colored as in panel (a); species with >33% declines or increases are labelled (see Table S1 for guide to species 4-letter codes).

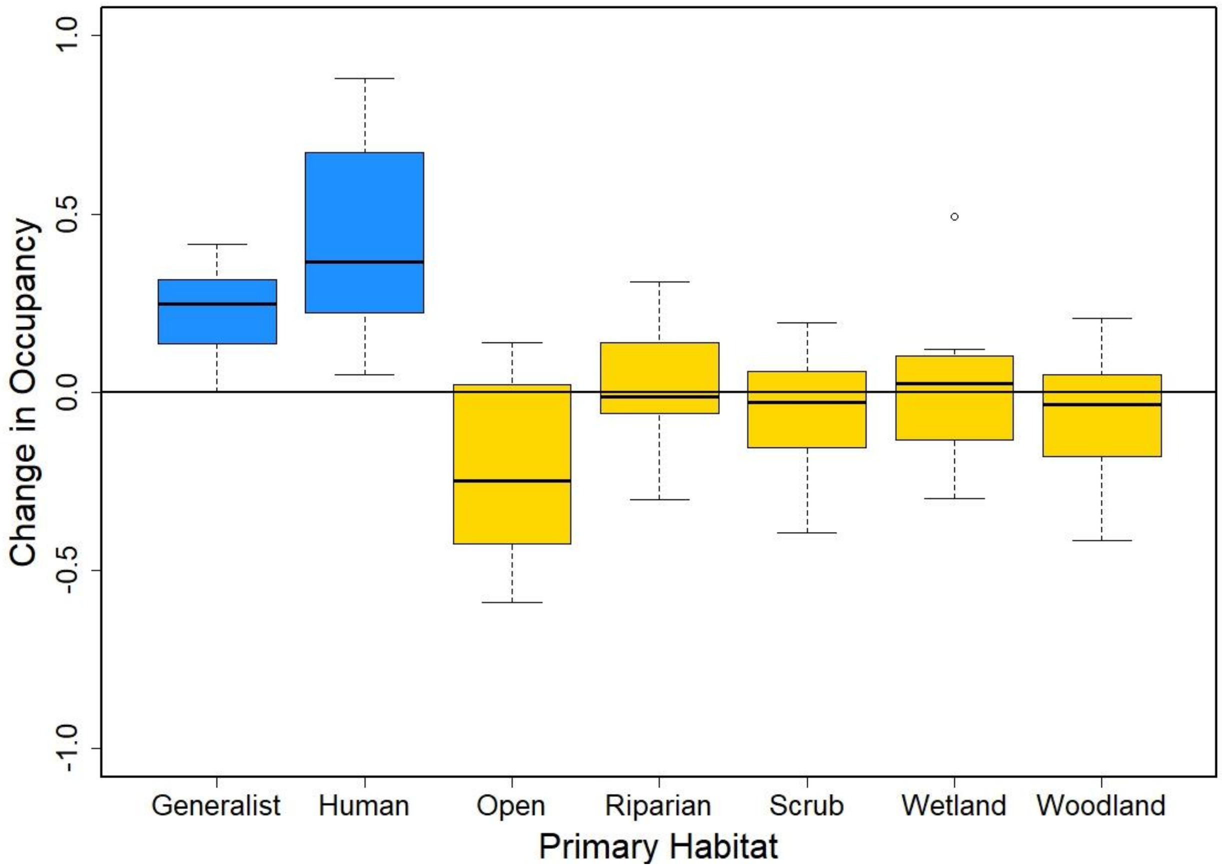


Figure 2: Changes in occupancy (modern – historic) by habitat preference. Although the full seven habitat categories are shown here for visualization purposes, our model set analyzed habitat as a binary variable separating species with generalist or human-associated habitat preferences (blue) from species preferring more specialized natural habitats (yellow).

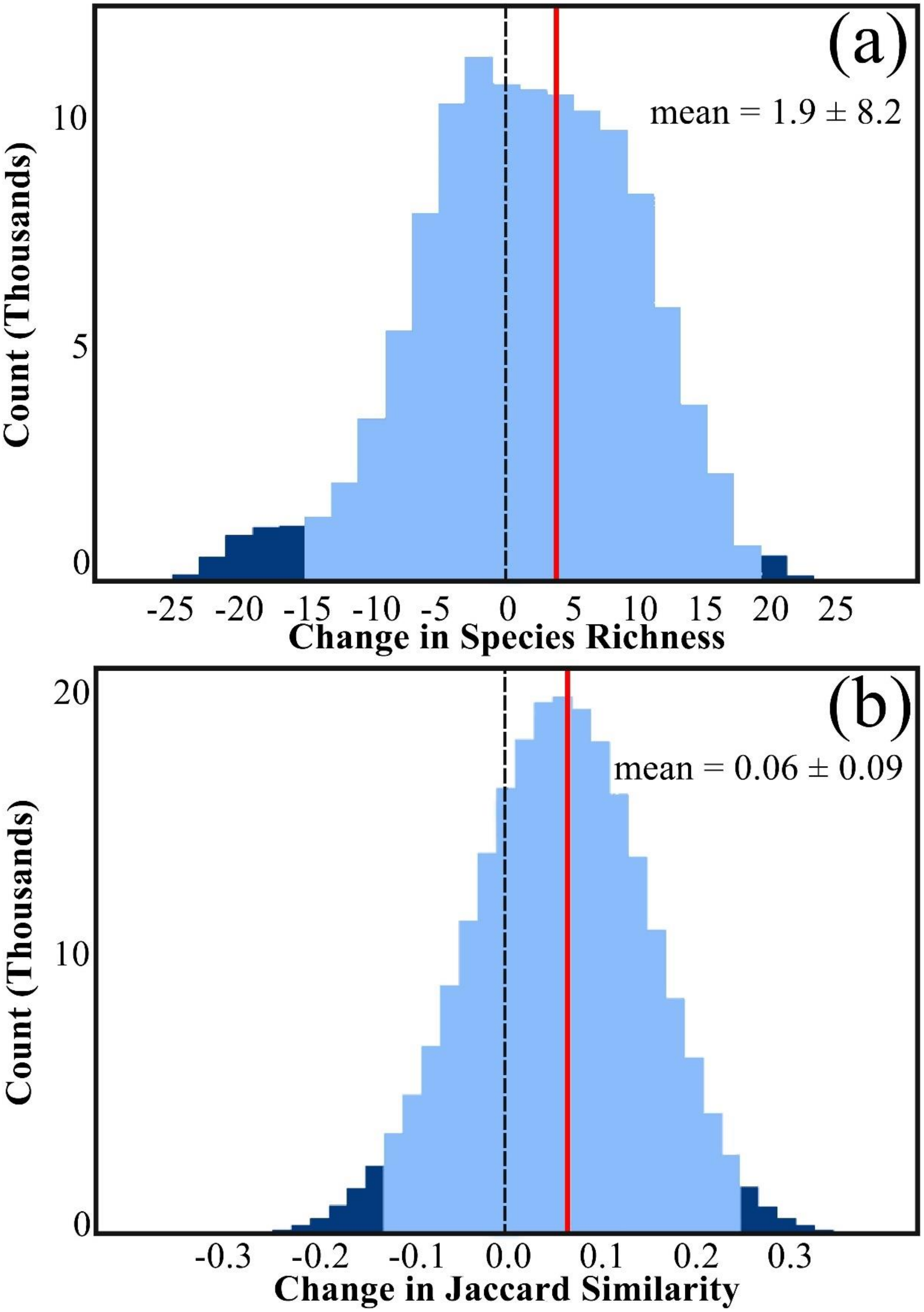


Figure 3: Histogram showing the posterior distribution for change (modern-historic) in (a) species richness per site and (b) Jaccard similarity between sites. Light blue regions indicate the 95% credible interval. Mean and one standard deviation are given for each distribution.

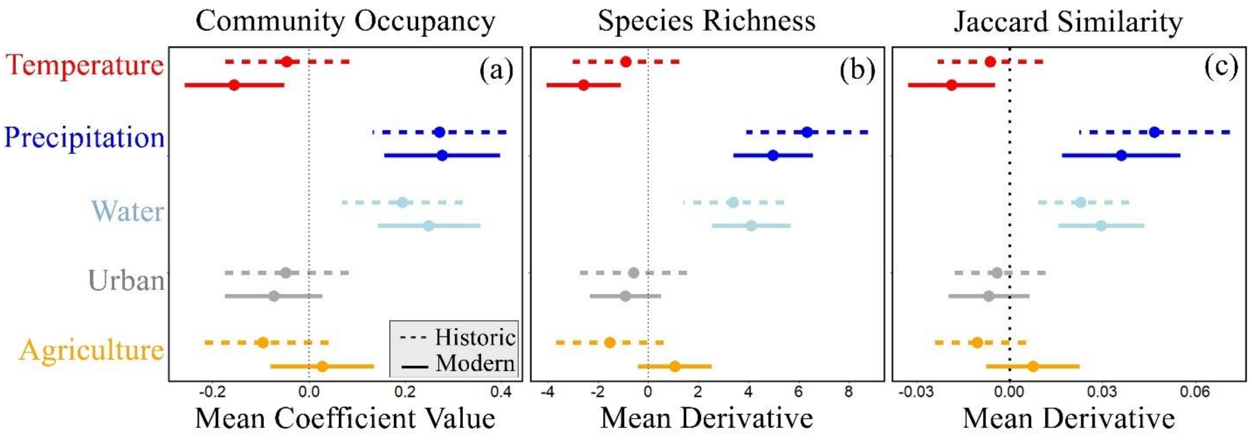


Figure 4: Effects of climate and habitat covariates on (a) community-level avian occupancy, (b) site-level species richness, and (b) Jaccard similarity between sites (c) in the historic (dashed) and modern (solid) survey periods. Lines represent 95% credible intervals. Panel (a) shows the community hyperdistribution (mean coefficient values of all species) from the occupancy model output. Panels (b) and (c) show the derivative at mean value for the effect of each covariate on expected species richness and similarity, approximated by the Monte Carlo method described in text.

Table S1: Species' specific changes in occupancy (modern – historic survey periods), and species' traits used in linear models as predictors of occupancy change. Species are designated using both their common name and 4-letter ABA code. Occupancy is given for the historic surveys, modern surveys, and change between surveys. Species' traits include habitat preference (1 = generalist or manmade habitat), body size (g), diet breadth (# of categories), and clutch size.

Code	Species	Historic	Modern	Change	Habitat	Size	Diet	Clutch
ACWO	Acorn Woodpecker *Melanerpes formicivorous*	0.55	0.53	-0.02	0	73	4	4
ALHU	Allen's Hummingbird *Selasphorus sasin*	0.04	0.00	-0.04	0	3	2	2
AMCO	American Coot *Fulica americana*	0.17	0.12	-0.05	0	900	3	10
AMCR	American Crow *Corvus brachyrhynchos*	0.22	0.52	0.30	1	450	7	5
AMGO	American Goldfinch *Spinus tristis*	0.67	0.14	-0.53	0	15.5	4	5
AMKE	American Kestrel *Falco sparverius*	0.83	0.15	-0.68	0	117	3	4.6
AMRO	American Robin *Turdus migratorius*	0.61	0.72	0.11	1	77	2	3
ANHU	Anna's Hummingbird *Calypte anna*	0.22	0.84	0.62	1	4.25	2	2
ATFL	Ash-throated Flycatcher *Myiarchus cinerascens*	0.69	0.85	0.16	0	28.5	3	4
BANS	Bank Swallow *Riparia riparia*	0.03	0.00	-0.03	0	14.5	1	4
BARS	Barn Swallow *Hirundo rustica*	0.50	0.36	-0.14	0	18.5	3	6
BCHU	Black-chinned Hummingbird *Archilochus alexandri*	0.08	0.18	0.09	0	3.1	2	2
BCNH	Black-crowned Night-heron *Nycticorax nycticorax*	0.30	0.35	0.04	0	800	4	4
BCSP	Black-chinned Sparrow *Spizella atrogularis*	0.04	0.00	-0.04	0	14.8	2	4
BEKI	Belted Kingfisher *Megaceryle alcyon*	0.14	0.25	0.11	0	150	4	6.5
BEVI	Bell's Vireo *Vireo bellii*	0.26	0.00	-0.26	0	9.8	2	4
BEWR	Bewick's Wren *Thryomanes bewickii*	0.55	0.63	0.09	0	9.8	2	6
BGGN	Blue-gray Gnatcatcher *Polioptila caerula*	0.51	0.19	-0.32	0	6.5	1	4
BHCO	Brown-headed Cowbird *Molothrus ater*	0.06	0.94	0.88	1	45	2	7
BHGR	Black-headed Grosbeak *Pheucticus melanocephalus*	0.50	0.45	-0.06	0	46	3	3
BLGR	Blue Grosbeak *Passerina caerula*	0.18	0.15	-0.03	0	28.5	4	4
BLPH	Black Phoebe *Sayornis nigricans*	0.54	0.87	0.33	1	18.3	1	4
BRBL	Brewer's Blackbird	0.63	0.86	0.23	1	64.5	1	5

	Euphagus cyanocephalus							
BRCR	Brown Creeper *Certhia americana*	0.00	0.02	0.02	0	8.55	3	5.7
BRSP	Brewer's Sparrow *Spizella breweri*	0.14	0.00	-0.14	0	11	2	3
BUOR	Bullock's Oriole *Icterus bullockii*	0.84	0.81	-0.02	0	36	3	5
BUOW	Burrowing Owl *Athene cunicularia*	0.40	0.00	-0.40	0	150	3	8
BUSH	Bushtit *Psaltriparus minimus*	0.68	0.76	0.07	0	5.5	4	6
CALT	California Towhee *Melozone crissalis*	0.66	0.75	0.09	0	47	4	3.5
CANG	Canada Goose *Branta canadensis*	0.04	0.35	0.31	1	4550	2	5
CANW	Canyon Wren *Catherpes mexicanus*	0.14	0.02	-0.12	0	18	1	5
CAQU	California Quail *Callipepla californica*	0.70	0.82	0.12	1	170	2	14
CATH	California Thrasher *Toxostoma redivivum*	0.50	0.14	-0.37	0	84.4	2	3
CAVI	Cassin's Vireo *Vireo cassinii*	0.20	0.09	-0.12	0	15.5	3	4.1
CEDW	Cedar Waxwing *Bombycilla cedrorum*	0.27	0.46	0.19	0	32	3	4
CHSP	Chipping Sparrow *Spizella passerina*	0.47	0.03	-0.44	0	13.2	2	4
CLSW	Cliff Swallow *Petrochelidon pyrrhonota*	0.49	0.87	0.38	1	23.2	1	4
COGD	Common Ground-dove *Columbina passerina*	0.00	0.02	0.02	0	35	3	2
COHU	Costa's Hummingbird *Calypte costae*	0.08	0.00	-0.08	0	3	2	2
CORA	Common Raven *Corvus corax*	0.29	0.78	0.49	1	1157	8	5
COYE	Common Yellowthroat *Geothlypis trichas*	0.53	0.18	-0.36	0	10.5	1	4
DEJU	Dark-eyed Junco *Junco hyemalis*	0.44	0.11	-0.33	0	19	2	4
DOWO	Downy Woodpecker *Picoides pubescens*	0.31	0.24	-0.07	0	24.5	3	5
EUCD	Eurasian Collard-dove *Streptopelia decaocto*	0.00	0.90	0.90	1	157	4	2
EUST	European Starling *Strunus vulgaris*	0.06	0.93	0.87	1	85	6	5
GBHE	Great Blue Heron *Ardea herodias*	0.71	0.44	-0.27	0	2300	4	4
GREG	Great Egret *Ardea alba*	0.03	0.55	0.52	0	1026	4	3
GRHE	Green Heron *Butorides virescens*	0.10	0.23	0.13	0	175	3	4
GRRO	Greater Roadrunner *Geococcyx californianus*	0.24	0.10	-0.14	0	284	5	4
GTGR	Great-tailed Grackle *Quiscalus mexicanus*	0.00	0.12	0.12	1	168	2	3

HAFL	Hammond's Flycatcher *Empidonax hammondii*	0.03	0.00	-0.03	0	10.4	1	3.5
HAWO	Hairy Woodpecker *Leuconotopicus villosus*	0.13	0.00	-0.13	0	85	4	4
HETH	Hermit Thrush *Catharus guttatus*	0.26	0.00	-0.26	0	27.8	2	4
HOFI	House Finch *Haemorhous mexicanus*	0.95	0.99	0.04	1	20.5	4	4
HOLA	Horned Lark *Eremophila alpestris*	0.60	0.26	-0.34	0	31	2	3.2
HOSP	House Sparrow *Passer domesticus*	0.44	0.73	0.29	1	28.5	3	5
HOWR	House Wren *Troglodytes aedon*	0.20	0.44	0.24	0	11	2	7
HUVI	Hutton's Vireo *Vireo huttoni*	0.09	0.10	0.01	0	11.3	3	4
KILL	Killdeer *Charadrius vociferus*	0.80	0.92	0.13	1	88	2	4
LAGO	Lawrence's Goldfinch *Spinus lawrencei*	0.25	0.50	0.24	0	11.5	2	4.5
LASP	Lark Sparrow *Chondestes grammacus*	0.84	0.49	-0.35	0	29	2	4
LAZB	Lazuli Bunting *Passerina amoena*	0.31	0.04	-0.28	0	15.2	2	4
LCTH	Le Conte's Thrasher *Toxostoma lecontei*	0.06	0.00	-0.06	0	61.8	2	3
LEGO	Lesser Goldfinch *Spinus psaltria*	0.60	0.65	0.05	1	9.2	4	4
LEWO	Lewis' Woodpecker *Melanerpes lewis*	0.09	0.00	-0.09	0	115	3	6
LOSH	Loggerhead Shrike *Lanius ludovicianus*	0.70	0.17	-0.53	0	46	4	5
MALL	Mallard *Anas platyrhynchos*	0.19	0.56	0.37	1	1082	5	9
MAWR	Marsh Wren *Cistothorus palustris*	0.04	0.09	0.05	0	11.5	1	5
MOBL	Mountain Bluebird *Sialia currucoides*	0.04	0.00	-0.04	0	29.6	3	5
MODO	Mourning Dove *Zenaida macroura*	0.70	0.99	0.29	1	133	2	2
MOUQ	Mountain Quail *Oreortyx pictus*	0.04	0.03	-0.01	0	233	3	11
NOFL	Northern Flicker *Colaptes auratus*	0.73	0.25	-0.48	0	170	3	6.5
NOHA	Northern Harrier *Circus cyaneus*	0.09	0.11	0.02	0	445	4	4.5
NOMO	Northern Mockingbird *Mimus polyglottos*	0.14	0.80	0.66	1	49	2	4
NRWS	Northern Rough-winged Swallow *Stelgidopteryx serripennis*	0.22	0.48	0.25	0	15.7	1	5.9
NUWO	Nuttall's Woodpecker *Picoides nuttallii*	0.45	0.79	0.34	0	37.4	4	4.5
OATI	Oak Titmouse *Baeolophusinornatus*	0.42	0.57	0.15	0	15.9	4	6
OSFL	Olive-sided Flycatcher *Contopus cooperi*	0.05	0.17	0.12	0	32.8	1	3

OSPR	Osprey *Pandion haliaetus*	0.00	0.08	0.08	0	1600	1	2.3
PHAI	Phainopepla *Phainopepla nitens*	0.21	0.19	-0.02	0	23	2	3
PIWO	Pileated Woodpecker *Hylatomus pileatus*	0.00	0.02	0.02	0	364	3	4
PSFL	Pacific-slope Flycatcher *Empidonax difficilis*	0.23	0.21	-0.02	0	10.5	2	3.5
PUMA	Purple Martin *Progne subis*	0.11	0.00	-0.11	0	48	1	5
RCKI	Ruby-crowned Kinglet *Regulus calendula*	0.18	0.00	-0.18	0	6.75	2	8
RCSP	Rufous-crowned Sparrow *Aimophila ruficeps*	0.06	0.06	-0.01	0	19	2	3
RNEP	Ring-necked Pheasant *Phasianus colchicus*	0.00	0.08	0.08	0	1263	4	11
ROPI	Rock Pigeon *Columba livia*	0.00	0.38	0.38	1	358	3	2
ROWR	Rock Wren *Salpinctes obsoletus*	0.11	0.08	-0.03	0	16.5	2	5
RRPA	Rose-ringed Parakeet *Psittacula krameri*	0.00	0.03	0.03	1	128	4	5
RSHA	Red-shouldered Hawk *Buteo lineatus*	0.06	0.31	0.26	0	625	3	3.5
RTHA	Red-tailed Hawk *Buteo jamaicensis*	0.78	0.92	0.14	0	1009	3	3
RWBL	Red-winged Blackbird *Agelaius phoeniceus*	0.66	0.64	-0.02	0	56	2	3.5
SAGS	Sage Sparrow *Artemisiospiza belli*	0.37	0.02	-0.35	0	17.1	2	3.4
SAPH	Say's Phoebe *Sayornis saya*	0.22	0.07	-0.14	0	24.1	2	4.5
SAVS	Savannah Sparrow *Passerculus sandwhicensis*	0.35	0.08	-0.27	0	15.9	4	4
SNEG	Snowy Egret *Egretta thula*	0.04	0.16	0.12	0	370	3	4
SOSP	Song Sparrow *Melospiza melodia*	0.50	0.30	-0.20	0	19.1	3	4
SPTO	Spotted Towhee *Pipilo maculatus*	0.49	0.58	0.08	0	40.4	3	3.7
STJA	Steller's Jay *Cyanocitta stelleri*	0.00	0.05	0.05	0	120	5	4
SWHA	Swainson's Hawk *Buteo swainsoni*	0.58	0.29	-0.29	0	980	3	3
TRBL	Tricolored Blackbird *Agelaius tricolor*	0.25	0.36	0.11	0	59.5	2	3
TRES	Tree Swallow *Tachycineta bicolor*	0.43	0.42	0.00	0	19	2	5
TUVU	Turkey Vulture *Cathartes aura*	0.93	0.63	-0.29	0	1430	1	2
VGSW	Violet-green Swallow *Tachycineta thalassina*	0.20	0.23	0.03	0	14.2	1	4.8
WAVI	Warbling Vireo *Vireo gilvus*	0.39	0.35	-0.04	0	12	2	3.5
WBNU	White-breasted Nuthatch *Sitta carolinensis*	0.28	0.33	0.05	0	20	2	8

WEBL	Western Bluebird *Sialia mexicana*	0.29	0.36	0.07	0	27.5	3	5
WEKI	Western Kingbird *Tyrannus verticalis*	0.79	0.98	0.19	1	40.7	2	4
WEME	Western Meadowlark *Sturnella neglecta*	0.93	0.45	-0.48	0	85	2	5
WESJ	Western Scrub-jay *Aphelocoma californica*	0.52	0.83	0.30	1	88.7	6	4
WETA	Western Tanager *Piranga ludoviciana*	0.02	0.29	0.27	0	34.5	2	4
WEWP	Western Wood-pewee *Contopus sordidulus*	0.20	0.30	0.10	0	13	2	3
WIFL	Willow Flycatcher *Empidonax traillii*	0.10	0.06	-0.05	0	12.6	2	3.5
WITU	Wild Turkey *Meleagris gallopavo*	0.00	0.16	0.16	0	7300	4	11
WIWA	Wilson's Warbler *Cardellina pusilla*	0.14	0.52	0.38	1	7	3	5
WREN	Wrentit *Chamaea fasciata*	0.18	0.13	-0.05	0	14.7	3	3.5
WTKI	White-tailed Kite *Elanus leucurus*	0.00	0.02	0.02	0	280	2	4.1
WTSW	White-throated Swift *Aeronautes saxatalis*	0.10	0.06	-0.04	0	31	1	4
YBCH	Yellow-breasted Chat *Icteria virens*	0.22	0.02	-0.20	0	26	2	5
YBMA	Yellow-billed Magpie *Pica nuttalli*	0.15	0.15	0.00	0	152	6	6.5
YEWA	Yellow Warbler *Setophaga petechia*	0.52	0.48	-0.04	0	16	1	4.3
YHBL	Yellow-headed Blackbird *Xanthocephalus xanthocephalus*	0.25	0.03	-0.22	0	75	1	3.6

Table S2: Mean and standard deviation for effects of climate and habitat covariates on community-level avian occupancy, site-level species richness, and Jaccard similarity between sites. Effects of covariates on occupancy are based on mean posterior coefficient values across all species in the occupancy model. Effects of covariates on richness and Jaccard similarity are based on derivatives at mean value, approximated by the Monte Carlo method described in text.

Metric	Era	Covariate	Mean	Standard Deviation
Occupancy	Historic	Temperature	-0.05	0.07
		Precipitation	0.27	0.07
		Water	0.20	0.07
		Urban	-0.05	0.07
		Agriculture	-0.10	0.07
	Modern	Temperature	-0.16	0.05
		Precipitation	0.28	0.06
		Water	0.25	0.06
		Urban	-0.07	0.05
		Agriculture	0.03	0.06
Richness	Historic	Temperature	-0.89	1.55
		Precipitation	6.33	1.60
		Water	3.39	1.55
		Urban	-0.59	1.30
		Agriculture	-1.52	2.31
	Modern	Temperature	-2.58	1.09
		Precipitation	4.97	1.13
		Water	4.12	2.28
		Urban	-0.91	0.93
		Agriculture	1.06	1.28
Jaccard Similarity	Historic	Temperature	-0.01	0.02
		Precipitation	0.05	0.02
		Water	0.02	0.02
		Urban	0.00	0.01
		Agriculture	-0.01	0.03
	Modern	Temperature	-0.02	0.01
		Precipitation	0.04	0.02
		Water	0.03	0.03
		Urban	-0.01	0.01
		Agriculture	0.01	0.02

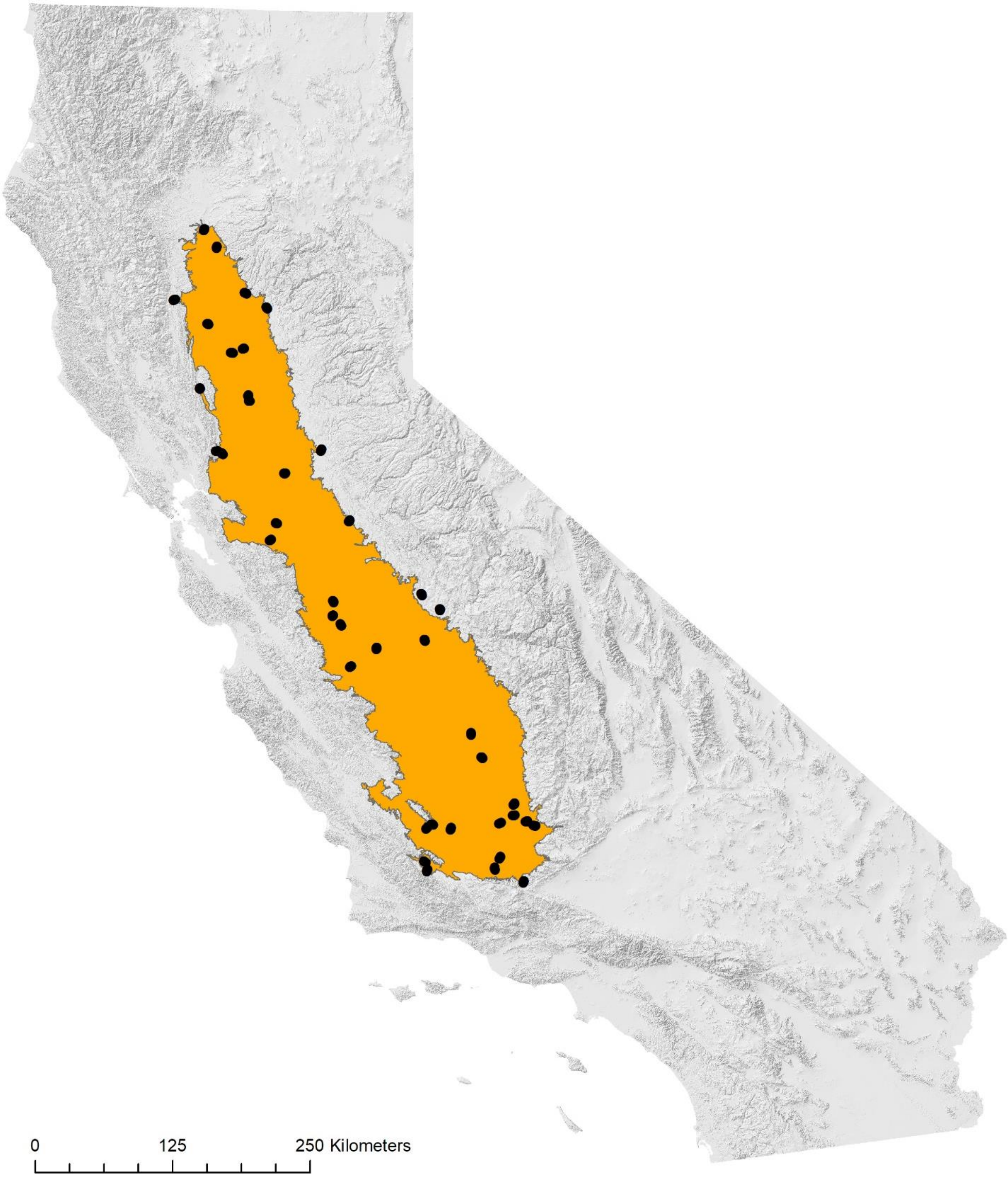
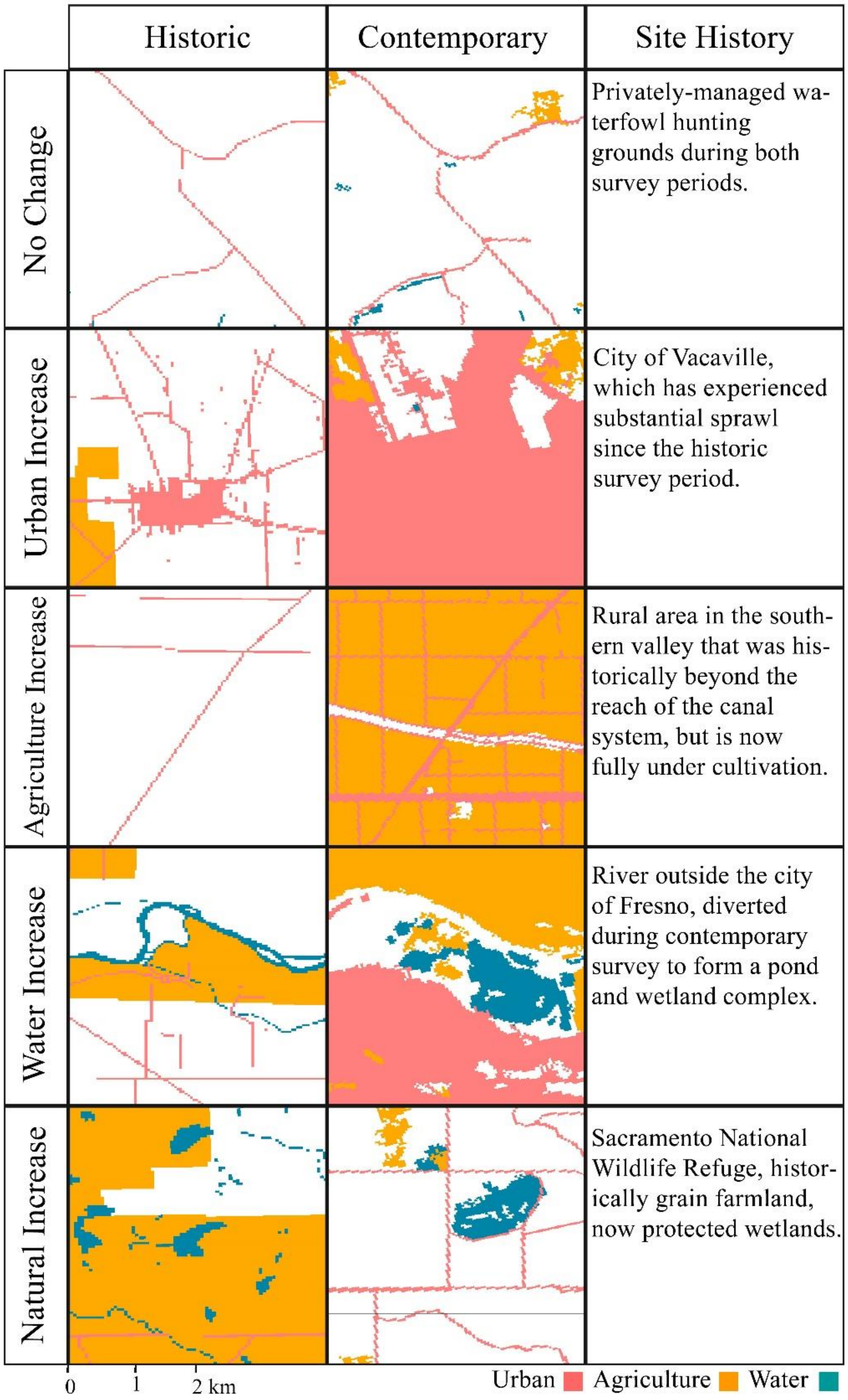


Figure S1: Map of survey locations. Shaded orange area represents the extent of the Central Valley ecoregion.



Privately-managed waterfowl hunting grounds during both survey periods.

City of Vacaville, which has experienced substantial sprawl since the historic survey period.

Rural area in the southern valley that was historically beyond the reach of the canal system, but is now fully under cultivation.

River outside the city of Fresno, diverted during contemporary survey to form a pond and wetland complex.

Sacramento National Wildlife Refuge, historically grain farmland, now protected wetlands.

Figure S2: Examples of change in urban, agriculture, and water coverage at five survey sites with varying land-use change histories, to demonstrate the efficacy of our historic mapping methods. Modern land-use data was obtained from the National Land Cover Dataset.

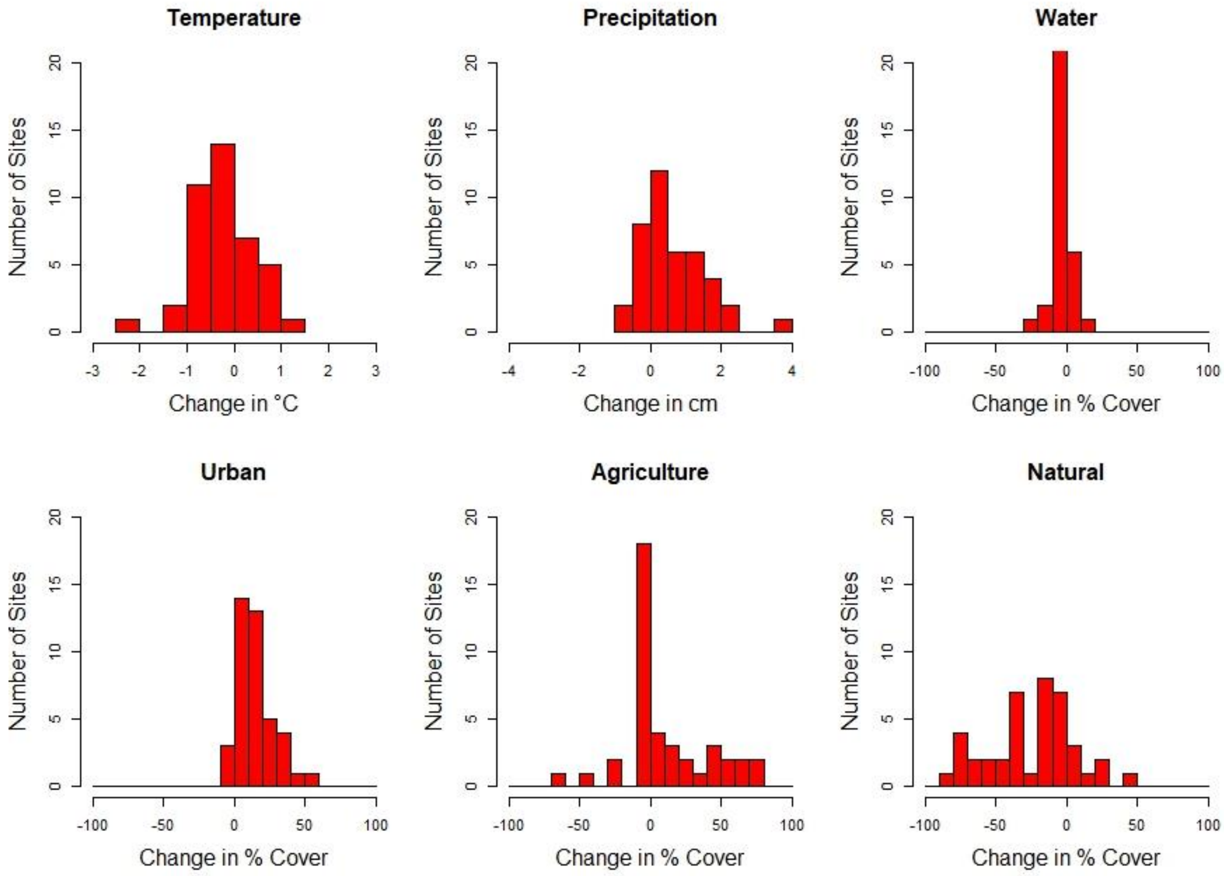


Figure S3: Site-level changes in maximum second quarter temperature, mean second quarter precipitation, and percent cover within 200m of water, urban, agriculture, and natural land use. for 41 sites in the California Central Valley between the historic (1912-1923) and modern (2015-2016) survey periods. All covariate values are unstandardized.

Appendix 1: Code for multispecies, single season occupancy model with covariates.

```
model{

#Define prior distributions for community-level model parameters

    omega ~ dunif(0,1)

# Mean and precision (tau) for community level distributions for species-level
# random effects

    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.a0 ~ dnorm(0,0.001)
    mu.a1 ~ 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.a0 ~ dgamma(0.1,0.1)
    tau.a1 ~ dgamma(0.1,0.1)

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

#Create priors for species i from the 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)

    a0[i] ~ dnorm(mu.a0, tau.a0)
    a1[i] ~ dnorm(mu.a1, tau.a1)
```

```
#Create a loop to estimate the Z matrix (true occurrence for species i
#at point j.

   for (j in 1:J) {
   logit(psi[j,i]) <- b0[i] + b1[i]*j_temp[j] + b2[i]*j_precip[j] + b3[i]*water[j] + b4[i]*urban[j] +
b5[i]*ag[j]

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

#Create a loop to 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]*dates[j,k]
           mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
  X[j,k,i] ~ dbern(mu.p[j,k,i])
  Xnew[j,k,i] ~ dbin(mu.p[j,k,i], 1)

#Create simulated dataset to calculate the Bayesian p-value
d[j,k,i]<-  abs(X[j,k,i] - mu.p[j,k,i])
dnew[j,k,i]<- abs(Xnew[j,k,i] - mu.p[j,k,i])
d2[j,k,i]<- pow(d[j,k,i],2)
dnew2[j,k,i]<- pow(dnew[j,k,i],2)

      }
dsum[j,i]<- sum(d2[j,1:K[j],i])
dnewsum[j,i]<- sum(dnew2[j,1:K[j],i])

  }}

#Calculate the discrepancy measure, which is then defined as the mean(p.fit > p.fitnew)
      p.fit<-sum(dsum[1:J,1:(n+nzeroes)])
      p.fitnew<-sum(dnewsum[1:J,1:n+nzeroes])


#Sum all species observed (n) and unobserved species (n0) to find the
#total estimated richness
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0

# Create a loop to determine point level richness estimates for the
# whole community and for subsets or assemblages of interest.
  for(j in 1:J){
    N_site[j]<- inprod(Z[j,1:n],w[1:n])
```

```
  }


#Estimation of Jaccard similarity index between sites (K is number of unique sites, K=41; M1
#and M2 are vectors of indices of paired
#sites).
for(j in 1:J2){
C[j]<-(inprod(Z[M1[j],1:n],Z[M2[j],1:n]))/ (sum(Z[M1[j],1:n])+sum(Z[M2[j],1:n])-
inprod(Z[M1[j],1:n],Z[M2[j],1:n]))
          }
}
```

Chapter 3.

Stability and decline: a century of climate and land-use change create divergent shifts in bird diversity of California's Central Valley and Los Angeles

Abstract

Climate and land-use change are two of the largest threats facing biodiversity, but the relative influence of these two drivers on species distributions is debated, as well as the degree to which communities have lost species diversity. We used a unique historic dataset – systematic early 20th century surveys of bird diversity conducted by Joseph Grinnell – paired with modern resurveys at 71 sites to analyze how avian occupancy and diversity have changed in the California Central Valley and Los Angeles, two adjacent regions with similar species composition but different histories of climate and land-use change. We used dynamic multispecies occupancy models to directly estimate the effects of climate and land-use on probabilities of initial occupancy, local persistence, and colonization. We found that occupancy, species richness, functional diversity, and phylogenetic diversity in the Central Valley all remained stable over the past century, despite large-scale agricultural development in this region. Los Angeles, a region that has undergone relatively more urban development, predominantly experienced declines in species occupancy and diversity. Changes in species occupancy were driven by habitat preference; generalists and human adapters primarily increased, while open country and forest species experienced the largest declines. Climate covariates were the major drivers of initial occupancy, while land-use change played the dominant role in local persistence, and both climate and land-use change drove colonization. Our findings demonstrate that the relative influence of climate and land-use change varies across different components of occupancy and turnover, and that their impact on diversity varies across species and regions.

Introduction

Climate and land use change are widely recognized as the greatest threats to biodiversity and ecosystem services (Maxwell et al. 2016, Scheffers et al. 2016). Realistic analyses of what drives biodiversity change – whether to dissect historical ecological trends or to project future distributions for conservation planning and policy – must consider the simultaneous effects of climate and land use rather than studying each in isolation (Martin et al. 2013, Ferger et al. 2017, Titeux et al. 2017).

To expand our understanding of the combined effects of land-use and climate change on biodiversity change, assessing the relative influence of these two drivers is an important first step (Martin et al. 2013, Bancroft et al. 2016, Titeux et al. 2016). The majority of current evidence suggests that climate is the dominant determinant of species distributions, with land-use having a comparably minor impact (Thuiller et al. 2004, Martin et al. 2013, Sohl 2014, Bucklin et al. 2015, Zamora-Gutierrez et al. 2017). In some systems, however, high levels of land-use change may override the effects of climate on species distributions (Bancroft et al. 2016, Karp et al.

2017), suggesting that there is still much to learn about the sources of heterogeneity in this relationship.

Considerable debate also exists concerning how biodiversity should be expected to change in response to climate and land-use change (Cardinale et al. 2018). The longest-standing and well-supported theory predicts species loss and homogenization in the face of global change (Newbold et al. 2015, Gonzalez et al. 2016). The combined effects of climate and land-use change exacerbate extinction risk compared to either driver independently (Jetz et al. 2007, Nuñez et al. 2013, Bonebrake et al. 2016), and reduce species richness and diversity by favoring similar groups of habitat generalists (Frishkoff et al. 2016). However, some recent analyses have challenged this assumption by claiming species richness is not declining at local spatial scales around the globe (Dornelas et al. 2014, Vellend et al. 2017). This debate will be greatly informed by continuing assessment of biodiversity change using high-quality datasets and more consideration for the identities of species experiencing turnover (Cardinale et al. 2018).

We analyzed how heterogeneous patterns of climate and land-use change drive changes in species occupancy, richness, and diversity. We used a unique historic resource – early 20th century systematic bird surveys conducted by Joseph Grinnell and colleagues– paired with contemporary resurveys to quantify the effects of climate and land-use change on avian diversity in the California Central Valley and Los Angeles basin. These two regions have experienced heterogeneous changes in temperature and precipitation since the early 1900s (Rapacciuolo et al. 2014). They provide examples of different land-use change histories – agricultural intensification has predominated in the Central Valley, while urbanization better characterizes Los Angeles. Protected areas with limited land-use change also occur in both regions. Specifically, we ask (1) how have bird species occupancy and diversity changed over the past century?; (2) were changes consistent across different diversity metrics (taxonomic, functional, and phylogenetic) and between survey regions?; and (3) what is the relative influence of climate versus land-use change on occupancy and turnover? We predicted that occupancy and diversity would decline more in Los Angeles than the Central Valley due to the greater extent of urbanization in the former, and that turnover would be driven predominantly by land-use change.

Methods

Study area

We studied changes in bird diversity in two of the most heavily transformed ecoregions in California: the Central Valley and Los Angeles. Combined, these two regions extend approximately 1000 km from north to south, and span an elevational gradient from sea level to 3500 m. The Central Valley is a low, flat landscape bordered on the east by the Sierra Nevada foothills and on the west by the Coast Ranges. The natural vegetation of the Central Valley is a mosaic of riparian belts and seasonal wetlands surrounded by grassland, oak woodland along the foothills, and saltbrush scrub in the southern valley (Nelson et al. 2003). Since the early 20th century, the Central Valley has become one of the most productive agricultural regions in the world (Sumner et al. 2003), with approximately 70 percent of its area under cultivation (Sleeter 2007).

Los Angeles is located within the South Coast ecoregion of California, which is separated from the Central Valley by the Transverse Ranges to the north and bordered by the Pacific Ocean to the west and by the Peninsular Ranges to the east. For the purposes of this paper, we use Los Angeles to refer to survey sites within Los Angeles County as well as the adjacent San Bernardino National Forest, which lies at the extreme southwest corner of San Bernardino county. The South Coast ecoregion is a hotspot for rare species in the United States (The Nature Conservancy 2000), and Los Angeles has the most recorded bird species of any county in the country (Sullivan et al. 2009). The natural vegetation of Los Angeles is predominantly chaparral and riparian (Barbour et al. 2007), and Los Angeles and the Central Valley have significant overlap in bird species associated with these two habitats. Los Angeles is distinct from the Central Valley in the former's relative scarcity of grassland, as well as greater coverage of coniferous woodland at higher elevation (Jin et al. 2013). Little agricultural development has occurred in Los Angeles over the past century, while urbanization has become dominant along the valley floor (Jin et al. 2013) and Los Angeles has grown to be the most populous county in the United States (U.S. Census Bureau 2010).

In addition to differences in land-use change histories, the Central Valley and Los Angeles have experienced heterogeneous patterns of climate change over the past century. Average annual temperature has increased throughout both regions, but by a greater amount in Los Angeles (Rapacciuolo et al. 2014). Annual precipitation has declined more in Los Angeles, whereas the Central Valley (mainly the northern half) has experienced increased precipitation (Rapacciuolo et al. 2014).

Bird surveys

We collected historic and modern bird survey data following standardized protocol for the Grinnell Resurvey Project (Tingley et al. 2009, 2012, Tingley and Beissinger 2013). To obtain data on historic localities and bird occupancy, we reviewed original field notebooks written by Joseph Grinnell and several of his colleagues, which are curated by the Museum of Vertebrate Zoology at UC Berkeley. These field notebooks provide detailed descriptions and maps of survey routes, as well as systematic lists of bird species observed each day. We identified 71 sites (42 Central Valley, 29 Los Angeles; Figure S1) with complete historic surveys of bird diversity. Historic surveys occurred from late March through July, between the years 1895 to 1908 in Los Angeles and 1912 to 1923 in the Central Valley. Each site had an average of 3.15 consecutive days of historic surveys (minimum 1, maximum 11).

We conducted modern resurveys during the breeding seasons (April through July) of 2015-2017 using standardized variable-distance point counts. For each site, we created a transect of 10 point count stops placed 250 m apart, corresponding as closely as possible to the area covered by the historic surveyors' camp and specimen collecting locations. Surveys began at dawn and lasted 2-3 hours. At each stop we recorded all birds seen or heard during a seven-minute period. Birds observed between point count stops were recorded if they were a new species for the day. Each site was surveyed daily over three consecutive days.

A total of 148 breeding bird species were included in our analysis. We excluded nocturnal birds, obligate waterbirds, and non-breeding birds, as these species were not sampled adequately by our survey protocol.

Climate and land-use covariates

We characterized climate at each site during each time period using both temperature and precipitation (Tingley et al. 2012). Climate data were obtained from 800 m resolution interpolated maps produced by the PRISM climate group (Daly et al. 2002), and averaged over 30-year periods corresponding to the historic (1900-1929) and modern (1988-2017) surveys. Annual minimum, annual maximum, and annual average temperature at our survey sites were highly correlated, so we chose to use annual average temperature in the interest of parsimony. We measured precipitation using total annual values.

We measured land use as percent cover of urban land, agricultural land, and water. These three focal land-use categories represent the dominant land-conversion processes that have occurred in the Central Valley and Los Angeles over the past century (Nelson et al. 2003, Jin et al. 2013). Change in area of natural land cover (i.e. grassland, wetland, scrub, riparian, and woodland) could not be quantified due to lack of historic data at a spatial and temporal resolution relevant to our project, but courser-scale mapping projects (Nelson et al. 2003) as well as qualitative descriptions in the historic field notes suggest there have been limited transitions among natural land cover types since the early 1900s. Therefore, we believe that our three focal land use categories adequately capture the processes of change most relevant to changes in bird occupancy. Historic land cover data were obtained by hand digitizing historic maps of urban land, agriculture, and water (Maclean *et al.* in review). Modern land cover data were obtained from the National Land Cover Database (Jin et al. 2013). Land cover covariates were calculated for a 200m buffer around the modern survey transects. A 200m buffer was chosen corresponding to the maximum distance at which bird species could be detected during the modern surveys. All continuous covariates were centered at 0 and normalized to a standard deviation of 1 prior to analysis.

Dynamic multispecies occupancy model

We used a dynamic multispecies occupancy model (MSOM) to explicitly estimate species' probability of occupancy, local colonization, and local persistence between the historic and modern survey periods (Royle and Kéry 2007, Dorazio et al. 2010). A multispecies model estimates species-specific values for each parameter or covariate effect while assuming all species effects come from a shared, community-level hyperdistribution for each parameter or coefficient (Iknayan et al. 2014). The model uses a hierarchical framework to estimate true occurrence of each species, while accounting for imperfect detection probability. Survey data y_{ijkt} (1 if present, 0 if absent) for the *i*-th species at the *j*-th site on the *k*-th visit in the *t*-th time period were assumed to result from imperfect observation of true incidence z_{ijt} (1 if present, 0 if absent). The probability of the survey data given true incidence and detection probability (p_{ijkt}) was:

$$y_{ijkt} | z_{ijt}, p_{ijkt} \sim Bernoulli\left(z_{ijt} p_{ijkt}\right).$$

Initial incidence z_{ij1} was modeled as a function of initial occupancy probability (ψ_{ik1}):

$$z_{ij1} | \psi_{ij1} \sim Bernoulli\left(\psi_{ij1}\right).$$

Probability of local persistence and colonization from the historic to the modern survey period were modeled as a first-order Markovian process, meaning that species incidence in the modern survey period was dependent on that species' incidence in the historic period. Incidence during the modern time period was modeled as a function of species' probability of local persistence (ϕ_{ikt}) and local colonization (γ_{ikt}) as follows:

$$z_{ij2} | z_{ij1}, \phi_{ij1}, \gamma_{ij1} \sim Bernoulli\left(\phi_{ij1} z_{ij1} + \gamma_{ij1}\left(1 - z_{ij1}\right)\right).$$

Each of the four probabilities (detection, initial occupancy, persistence, colonization) were modeled as a linear combination of site and/or survey period covariates using a logit-link transformation:

$$\begin{aligned} logit\left(p_{ijkt}\right) &= \alpha_{0i} + \boldsymbol{\alpha_i W_{jkt}} \\ logit\left(\psi_{ij1}\right) &= \beta_{0i} + \boldsymbol{\beta_{i1} X_{j1}} \\ logit\left(\phi_{ij}\right) &= \delta_{0i} + \boldsymbol{\delta_i Y_j} \\ logit\left(\gamma_{ij}\right) &= \epsilon_{0i} + \boldsymbol{\epsilon_i Z_j} \end{aligned}$$

where naught terms represent the species-specific intercept for each probability, the bold terms on the left represent arrays of species-specific coefficients, and the bold terms on the right represent arrays of the associated covariate values.

Following previous MSOMs for birds in California (Tingley and Beissinger 2013), detection probability was modeled as a function of Julian day (jday = 1 on 1 January) and its quadratic. To account for differences in detection between historic and modern surveyors (Tingley and Beissinger 2009), we also modeled detection probability as a function of survey era (binary). Initial occupancy was modeled as a linear function of average annual temperature, annual precipitation, percent cover of water, percent cover of urbanization, and percent cover of agriculture. Probability of persistence and colonization were both modelled as a function of change in temperature, precipitation, urban, and agriculture. Change in percent cover of water was not included as a covariate for persistence or colonization because the range of values was small (Figure 1, Table 1), and models had difficulty converging.

Data were pre-processed in R version 3.4.3 and Bayesian parameter estimation was implemented using MCMC in JAGS via the package "jagsUI". We used uninformative priors for the hyper-distributions of the intercept terms and means of the coefficients. For the variances of the hyper-distributions, we used weakly-informative priors as a type of regularization known as shrinkage (Hooten and Hobbs 2015). The full model code is provided in Appendix 1. Models were fully adapted (n = 200). We ran four parallel chains of length 20000, discarding the first 10000 as burn-in, and used a thinning rate of 10. This resulted in a posterior distribution consisting of 4000 samples for each parameter. Convergence was assessed by visual inspection of trace plots and by using the Gelman-Rubin convergence diagnostic (Gelman and Hill 2007). All diagnostic values were ≤ 1.1, which satisfies the criteria for convergence.

Species traits

Heterogeneity in species-specific responses to climate and land-use change can be explained to different degrees by functional and life history traits (Angert et al. 2011, Estrada et al. 2016). We tested the strength of traits as predictors of mean change in species' occupancy between the historic and modern survey periods. We focused on five of the most frequently tested and supported traits relevant to changing species' distributions: habitat use, diet, migratory behavior, log-transformed body size, and tolerance for human habitat modifications (MacLean and Beissinger 2017). The complete dataset of species' traits is presented in Table S1. Trait data were obtained from The Birds of North America Online (Rodewald 2015), the online Encyclopedia of Life (Parr et al. 2014), and Elton Traits (Wilman et al. 2014).

We modeled change in species-specific occupancy as a function of each individual trait using linear mixed effects models, with species as a random effect. To account for model uncertainty, we weighted each measure of mean occupancy change by the inverse variance of its posterior distribution. Models with combinations of two or more traits never performed better than single-trait models, so we excluded these from our final model set. We compared the full model set (n=6) using AIC_c.

Species diversity

To account for the multiple facets of biodiversity (Jarzyna and Jetz 2016), we calculated several metrics of species taxonomic, functional, and phylogenetic diversity change between the historic and modern survey periods. All metrics were calculated using true incidence z_{ijt} as estimated from the MSOM and repeated for all 4000 samples of the posterior distribution to account for model uncertainty.

Species richness $N_{j,t}$ was calculated simply as the sum of species per site:

$$N_{jt} = \sum_{i=1}^{148} z_{ijt}$$

We measured similarity in species composition between sites (*a* and *b*) using the Sorensen index (Sørensen 1948, Tucker et al. 2016):

$$S_{ab} = \frac{2\sum_{i=1}^{n} z_{ita} z_{itb}}{N_a + N_b}$$

We calculated functional diversity using a set of 17 ecological and life-history traits (Barnagaud et al. 2017). The traits fell into three categories: (1) ecological traits (main habitat category, nest location, foraging strategy, main diet category, tolerance of human habitat modification); (2) life-history traits (territory type, migratory behavior category, developmental mode, mean log-transformed body mass, mean wingspan, mean body length); and (3) reproductive traits (number of broods per year, mean clutch size, mating behavior, altricial or precocial development, maximum lifespan).

We created a dendrogram of all 148 species in our surveys based on the full trait set (Petchey and Gaston 2006, Barnagaud et al. 2017). We then quantified trait diversity for the subset of species present at each site using Faith's PD (Faith 1992), which measures the total length of all branches in a dendrogram. Because absolute PD for functional diversity (trait PD_{abs}) is highly correlated with species richness (Tucker et al. 2016), we also calculated PD relative to the number of species present at the site (trait PD_{rel}) following Davies et al. (2007).

To calculate phylogenetic diversity at each site, we downloaded 100 trees using Hackett backbones from birdtree.org (Jetz et al. 2012, 2014). For each tree, we created a dendrogram of all 148 species in our surveys, then calculated phylogenetic diversity for the subset of species at each site using Faith's PD. Similar to calculations for functional diversity, we calculated both absolute PD (phylo PD_{abs}) and relative PD (phylo PD_{rel}).

Results

Climate and land-use change

Survey sites in the California Central Valley and Los Angeles experienced divergent changes in climate and land-use over the past century (Figure 1, Table 1). Historically, survey sites in the Central Valley were significantly hotter and dryer than sites in Los Angeles (Student's t-test for difference in temperature, $t = 3.06$, $df = 31$, $p < 0.01$; precipitation $t = -6.07$, $df = 59$, $p < 0.001$). Since the historic surveys, Central Valley sites experienced an average of 1 °C less warming than Los Angeles sites ($t = -17.40$, $df = 57$, $p < 0.001$). At the same time, Central Valley sites became wetter on average, while Los Angeles sites became dryer ($t = 11.26$, $df = 38$, $p < 0.001$).

Historic coverage of urbanization was similar in Los Angeles and the Central Valley ($t = 1.40$, $df = 52$, $p = 0.17$) as were percent cover of agriculture ($t = 0.20$, $df = 61$, $p = 0.84$) and water ($t = 2.38$, $df = 58$, $p = 0.02$). Over the past century, however, urbanization increased significantly less in the Central Valley compared to Los Angeles ($t = -3.42$, $df = 32$, $p < 0.01$), whereas agriculture increased significantly more at sites in the Central Valley ($t = 3.56$, $df = 67$, $p < 0.001$). Percent cover of water changed little in both regions ($t = -0.95$, $df = 56$, $p = 0.35$).

Change in bird species' occupancy

Species composition was very similar between the Central Valley and Los Angeles: of the 148 species in our dataset, 7 (4.7%) were recorded only in the Central Valley and 11 (7.4%) were recorded only in Los Angeles.

Species occupancy declined more over the past century in Los Angeles than the Central Valley (Figure 2). Occupancy in the Central Valley was relatively stable, with a mean change across all species of -0.02 ± 0.01. Of the 148 species analyzed, 38 (25.7%) showed a significant decrease in occupancy in the Central Valley, 30 (20.3%) had a significant increase, and 80 (54.0%) did not change significantly. In Los Angeles, however, mean occupancy across species decreased by -0.14 ± 0.01, with 75 species (50.1%) experiencing a significant decrease, 20 (13.5%) a significant increase, and 53 (35.8%) no change.

The top increasing species in both regions were predominantly exotics and native species that were tolerant of human habitat modification. These included the brown-headed cowbird, European starling, Eurasian collared-dove, Anna's hummingbird, common raven, rock pigeon, northern mockingbird, and great egret (Figure 3; see Table S2 for scientific names). The top declining species in the Central Valley were predominantly open-country birds including the American kestrel, lazuli bunting, loggerhead shrike, western meadowlark, savannah sparrow, American goldfinch, lark sparrow, and turkey vulture. While the American kestrel and turkey vulture were also the top declining species in Los Angeles, otherwise the biggest declines in this region were for forest and riparian species such as hermit thrush, chipping sparrow, Cassin's vireo, Bullock's oriole, and ruby-crowned kinglet. Nine species increased significantly in the Central Valley but decreased significantly in Los Angeles: western kingbird, Brewer's blackbird, American robin, black phoebe, house wren, Lawrence's goldfinch, brown creeper, western tanager, and mourning dove. In contrast, no species increased significantly in Los Angeles but decrease in the Central Valley.

Species-level changes in occupancy were driven by habitat preferences (Table 3). Differences in the primary habitat used by each species explained almost all of the variation in occupancy change (AIC_c weight = 1.00) relative to body size, migratory behavior, diet, or tolerance of human habitat modification. In both Los Angeles and the Central Valley, occupancy increased for habitat generalists and species that prefer developed areas (Figure 4). Mean occupancy change was similar across species found in natural habitat types, though the largest declines were by open country species in the Central Valley and by open country and forest species in Los Angeles.

Change in community diversity

Species diversity changed little over the past century in the Central Valley (Figure 5, Table 2). Average historic richness was 46.7 species per site (95% credible interval = 28.7 – 64.7) and declined modestly by an average of 3.2 species per site (CI = -5.5 − -0.9). Historic species diversity between sites in the Central Valley, as measured by the Sorensen index, did not change significantly (Table 2). There were also no significant changes over the past century in absolute functional diversity, relative functional diversity, absolute phylogenetic diversity, or relative phylogenetic diversity (Table 2).

Survey sites in Los Angeles predominantly experienced a large loss of avian diversity over the past century (Figure 5, Table 2). Average species richness during the historic survey period was 63.8 species per site (CI = 43.7 – 83.9) and declined by 22.5 species per site (CI = -24.8 – -20.1). Sorensen diversity between sites declined on average by 0.11 per site pair (CI = -0.13 – -0.09). There were also significant declines in absolute functional diversity (CI = -1.87 – -0.22) and absolute phylogenetic diversity (CI = -790.25 – -86.11). However, there were no significant changes in relative functional diversity or relative phylogenetic diversity (Table 2).

Relative effects of climate and land-use change on turnover

Occupancy in the early 20th century was driven primarily by climate covariates (Figure 6). Temperature had the greatest community-level effect (coefficient hyperdistribution mean = 0.57, CI = 0.32 − 0.82) and the largest number of species with significant coefficient effects (n = 48 positive, 9 negative). Precipitation had a large, but not quite significant, community-level effect (mean =0.27, CI = -0.03 − 0.57), with a roughly equal number of significant positive and negative species-level coefficient effects (n = 28 positive, 20 negative). Percent cover of water had a minimal community-level effect, but a few species with significant effects (n = 8 positive, 4 negative). Percent cover of urbanization and agriculture had minimal community-level effects and no individual species with significant effects.

Turnover (co1lonization and persistence) was driven by both climate and land-use change (Figure 6). Temperature change had the greatest effect on probability of colonization, and sites that warmed gained species (hyperdistribution mean = 0.93, CI = 0.64 − 1.22; n = 21 species positive, 0 negative). Change in percent cover of urbanization was the second most influential factor, attracting species that benefitted from human habitation (hyperdistribution mean = 0.40, CI = 0.17 −0.63 ; n = 11 species positive, 0 negative). Change in precipitation had no significant community-level effect on colonization and only six significant species effects (n = 5 positive, 1 negative, while change in percent cover of agriculture no significant community or species-level effects. Probability of persistence was driven primarily by change in percent cover of urbanization (hyperdistribution mean = -0.47, CI = -0.69 − -0.26; n = 0 species positive, 16 negative). Change in temperature had the second most significant species-level effects (n = 9 positive, 2 negative), but no significant community-level effect. Precipitation and agriculture again had limited effects on persistence.

Discussion

Our findings challenge the idea that there is a single general rule to biodiversity change in altered landscapes, and to the relative influence of climate and land-use change on species distributions. Over the past century, avian responses to climate and land-use change in the California Central Valley and Los Angeles have varied by species and region. We found evidence for both diversity decline and stability, caused by differences in how climate and land-use affected components of turnover.

Changes in species occupancy differed between regions affected by urbanization and agriculture

Despite similar species composition, geographic proximity, and shared histories of human habitat modification, birds of the Central Valley and Los Angeles experienced very different patterns of change over the past century. The Central Valley avifauna was relatively stable, with declining species roughly balanced by increasing species (Figure 2a) which resulted in little change to community diversity (Figure 5). Sites in Los Angeles historically had greater diversity than the Central Valley, but experienced larger declines in species occupancy (Figure 2b) and diversity (Figure 5), which has resulted in modern diversity that is similar to the Central Valley. Our findings confirm that climate and land-use change are not universally accompanied by biodiversity loss, but instead may result in either decline (Newbold et al. 2015, Gonzalez et al. 2016) or stability (Dornelas et al. 2014, Vellend et al. 2017) depending on the geographic context, even in very similar regions and taxa.

Even when biodiversity has not declined, important changes in species composition may still occur (Prendergast et al. 1993, Kerr 1997, Cardinale et al. 2018). Though diversity remained stable in the Central Valley, there was high species turnover (Figure 2a). Increasing species were predominantly generalists and synanthropic species, while declining species mostly used open habitats (Figure 4a), a common trend in landscapes experiencing land-use change (McKinney 2002, Bonebrake et al. 2016, Frishkoff et al. 2016). This pattern was similar in Los Angles, but open habitat species and additionally forest species experienced even larger declines (Figure 4b). Though species-level occupancy changes in Los Angeles and the Central Valley were strongly related (Figure 3), species declined more strongly in Los Angeles (Figure 3). No species experienced a significant increase in Los Angeles and decrease in the Central Valley, but the converse was true for an interesting subset of species: mourning dove, western tanager, house wren, Lawrence's goldfinch, black phoebe, American robin, western kingbird, and Brewer's blackbird. These birds are more tolerant of agricultural modification than urbanization (Rodewald 2015), further demonstrating that heterogeneity in the type of regional land-use change causes heterogeneity in biodiversity change.

Some additional species changes are noteworthy despite relatively small overall changes in occupancy. Several species of conservation concern were present at low or moderate occupancy during historic surveys, but were detected sparingly or not at all during modern surveys. These included the state endangered California gnatcatcher and Bell's vireo, and the yellow-breasted chat, a species of special concern (California Department of Fish and Wildlife 2017). Several exotic species colonized California after the historic surveys, including top increasing species such as the Eurasian collared-dove, brown-headed cowbird, rock pigeon, and great-tailed grackle. Other colonizing exotic species currently remain limited to localized populations, including the wild turkey and ring-necked pheasant in the Central Valley, and red-crowned parrot, Indian peafowl, red-whiskered bulbul, and yellow-chevroned parakeet in Los Angeles. Several additional exotic species were detected during modern surveys but were not included in our dataset due to limited population establishment, including the rose-ringed parakeet in the Central Valley, and the northern cardinal, Egyptian goose, blue-fronted parrot, and scaly-breasted munia in Los Angeles. Over the coming century, these exotic species will likely continue to establish and expand, particularly in Los Angeles (Butler 2005).

Climate and land use influence different components of turnover

Both climate and land-use change – primarily temperature and urbanization – emerged as major drivers of bird occupancy, and their relative influence differed for initial occupancy, colonization, and persistence (Figure 6). Bird occupancy in the early 1900s in the Central Valley and Los Angeles was driven mainly by climate. Strong effects of temperature and precipitation likely reflect (1) sensible adaptations of bird species to the semi-arid climate shared by these two regions, and (2) the minimal effects of urbanization and agriculture on initial occupancy, evidenced by the limited land coverage of these altered habitats during the historic survey period (Figure 1). In contrast, change in percent cover of urbanization was a major driver of both colonization and persistence. Climate covariates had less relative influence on rates of turnover, with temperature reduced to a major driver only for colonization, and precipitation having limited influence on either colonization or persistence.

Our results add to a growing body of literature that supports climate as a dominant driver of species distributions in systems with limited land-use change (Martin et al. 2013, Sohl 2014, Bucklin et al. 2015), but also supports species distributions driven strongly by land-use change in heavily-transformed regions (Karp et al. 2012, 2017, Bancroft et al. 2016, Zamora-Gutierrez et al. 2017). Thus, to accurately forecast species distributions, the influence of both climate and land-use change must be considered (Ferger et al. 2017, Titeux et al. 2017). Moreover, our results suggest that climate and land-use change may vary in their relative influences, not only among species and between geographic regions, but also in how they differentially affect occupancy and turnover.

Covariate effects also revealed a shift towards bird communities with more warm- and urban-adapted species. Species with high probabilities of colonization were primarily warm-weather species and those tolerant of urbanization (Figure 6), a trend with support from other systems experiencing anthropogenic change (Breed et al. 2012, Princé and Zuckerberg 2014, Payne and Smith 2016, Scheffers et al. 2016). In comparison, local extinction was driven primarily by intolerance of urbanization. These heterogeneous species-level effects manifested in detectable changes in diversity only in Los Angeles and not the Central Valley. Systems with high species turnover may show stability in taxonomic diversity (i.e. species richness) that masks loss of functional or phylogenetic diversity as native specialists are replaced by exotic generalists (Karp et al. 2011, Frishkoff et al. 2014, Sol et al. 2017). Whereas all three metrics declined in Los Angeles (Figure 5), we were surprised to find no change in taxonomic, functional, or phylogenetic diversity of the Central Valley. Nevertheless, changes in species composition without concomitant biodiversity loss are still important for conservation planning (Prendergast et al. 1993, Kerr 1997, Marzluff et al. 2001).

Implications for conservation

Patterns of distributional change are highly heterogeneous across species with different tolerances for environmental change (Estrada et al. 2016, MacLean and Beissinger 2017), and in regions with different histories of climate and land-use change. A better understanding of this heterogeneity is important for the theoretical bases of spatial and community ecology, and also for practical applications in biodiversity conservation and policy (Leadley et al. 2010, Titeux et al. 2017). Projections of future biodiversity loss have primarily been created using broad-scale species distribution models based on current climate envelopes (Thomas et al. 2004, Elith and Leathwick 2009). These models often fail to incorporate the influences of land-use change, species' traits, or other important drivers that shape species distributions (Araújo et al. 2005, Peterson et al. 2007, Angert et al. 2011). Ideally, distributional models and projections should incorporate the combined effects of climate change, land-use change, and heterogeneous species responses, with values derived from observed historical changes. This will not always be feasible, but should be the goal whenever possible.

Urban land cover in the United States is projected to expand much more rapidly over the coming century than is agricultural land (Sleeter et al. 2012), and megacities such as Los Angeles are creating unprecedented pressure on biodiversity in urban areas (Kraas 2008). Given the prospect of an increasingly urbanized future, our findings that diversity declined much more in Los Angeles (a major urban region) than in the Central Valley (a major agricultural region) are particularly alarming. Regardless of biodiversity loss, both the Central Valley and Los Angeles also experienced substantial species turnover, a process that is equally important to conservation. Non-analog communities are projected to become increasingly prevalent in California over the coming century (Stralberg et al. 2009), and increased competition due to changing community composition may be as large a threat as direct habitat conversion to some species (Cahill et al. 2012).

Despite our findings of lost diversity in Los Angeles and declining specialist species in both regions, the concomitant persistence of some native species in altered habitats is encouraging. The stability of avian diversity over the past century at our Central Valley sites is likely related to the preference of historic surveyors for riparian study sites, many of which remain as fragmented habitats (Nelson et al. 2003). Some types of human landscaping, water supplementation, and bird feeding in parks and suburban areas may also provide refugia from climate or land-use change (Morelli et al. 2012, 2016, Greig et al. 2017). In Los Angeles, bird species richness increased at only one survey site – a small river restoration park heavily landscaped with native vegetation. More research is needed to explore how different practices of urban landscaping may improve the ability of species to persist in altered habitats (Cannon et al. 2005, Chamberlain et al. 2009).

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Table 1: Values for initial covariates and covariate change at each site, separated by region. Bolded values were significantly different between the Central Valley and Los Angeles.

	Central Valley		Los Angeles	
Covariate	Historic	Change	Historic	Change
Temperature (°C)	**15.87 ± 0.20**	**0.88 ± 0.03**	**13.63 ± 0.24**	**1.80 ± 0.04**
Precipitation (mm)	**368.72 ± 26.95**	**11.18 ± 3.23**	**621.92 ± 32.43**	**-77.20 ± 3.89**
Urban Cover (%)	0.08 ± 0.01	**0.13 ± 0.02**	0.05 ± 0.01	**0.39 ± 0.02**
Agriculture Cover (%)	0.12 ± 0.04	**0.30 ± 0.05**	0.11 ± 0.05	**-0.11 ± 0.06**
Water Cover (%)	0.05 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	-0.01 ± 0.01

Table 2: Mean and 95% credible intervals of the posterior distributions for historic, modern, and change in species richness per site, Sorensen diversity between sites, absolute functional diversity (FD), relative functional diversity, absolute phylogenetic diversity (PD), and relative phylogenetic diversity.

	Region	Historic	Modern	Change
Richness	Central Valley	46.7 ± 18.0	43.5 ± 20.6	-3.2 ± 2.3
	Los Angeles	63.8 ± 20.5	41.3 ± 13.5	-22.5 ±2.4
Sorensen	Central Valley	0.53 ± 0.23	0.55 ± 0.22	0.02 ± 0.02
	Los Angeles	0.61 ± 0.28	0.50 ± 0.29	-0.11 ± 0.02
Absolute FD	Central Valley	3.3 ± 0.9	3.3 ± 1.2	0.0 ± 0.9
	Los Angeles	3.9 ± 0.9	2.9 ± 0.9	-1.0 ± 0.8
Relative FD	Central Valley	0.07 ± 0.01	0.08 ± 0.01	0.00 ± 0.01
	Los Angeles	0.06 ± 0.01	0.07 ± 0.01	0.01 ± 0.01
Absolute PD	Central Valley	1580 ± 443	1497 ± 553	-84 ± 429
	Los Angeles	1776 ± 421	1337 ± 402	-438 ± 359
Relative PD	Central Valley	34.9 ± 7.1	35.1 ± 7.1	0.7 ± 6.8
	Los Angeles	28.1 ± 5.5	32.5 ± 5.0	4.3 ± 6.4

Table 3: AICc rankings for linear mixed effects models of traits as predictors of occupancy change, weighted by variance in occupancy change.

Model	k	AICc	ΔAICc	AICc Weight	Log Likelihood
Habitat	7	28.29	0	1.00	-6.75
Human tolerance	3	50.93	22.65	0.00	-22.39
Migratory behavior	4	101.07	72.78	0.00	-46.40
Diet category	8	109.37	81.08	0.00	-46.17
Body size	3	113.27	84.98	0.00	-53.55
Null	2	116.33	88.04	0.00	-56.13

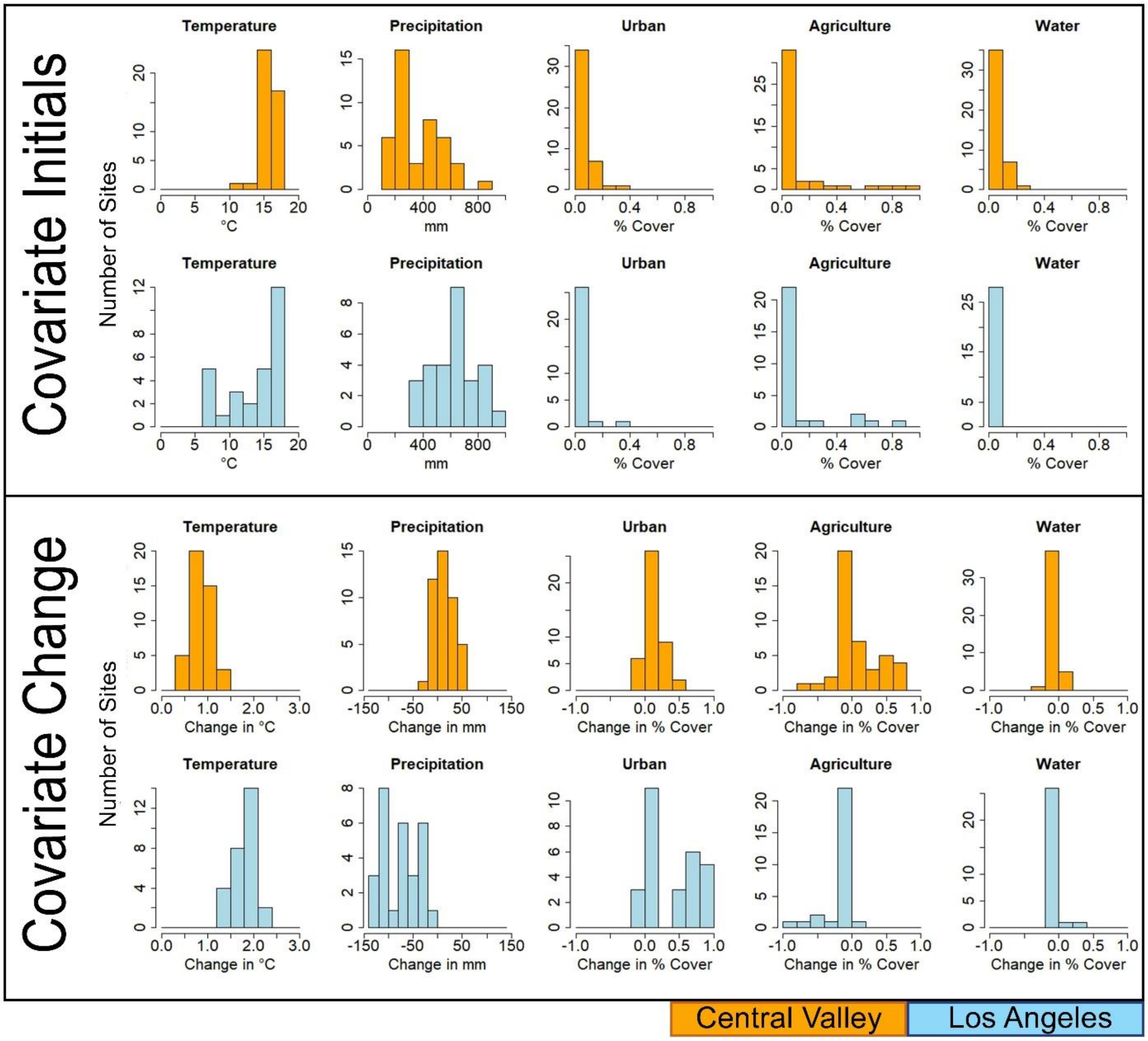

Figure 1: Values for initial covariates and covariate change at each site, separated by region.

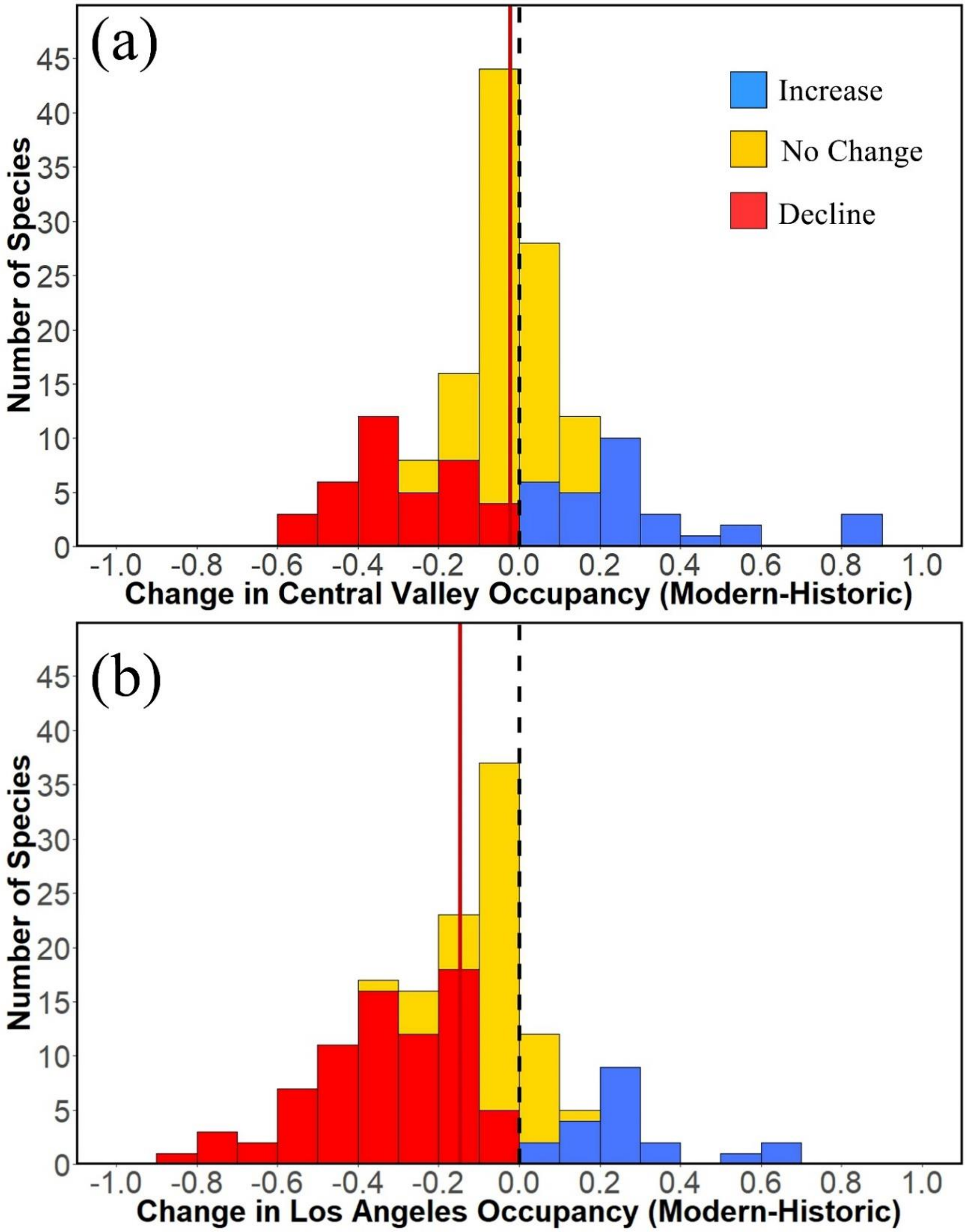

Figure 2: Change in occupancy for 148 bird species in the California Central Valley and Los Angeles. Colors indicate statistical significant of species-specific change. Red lines indicate the mean across all species.

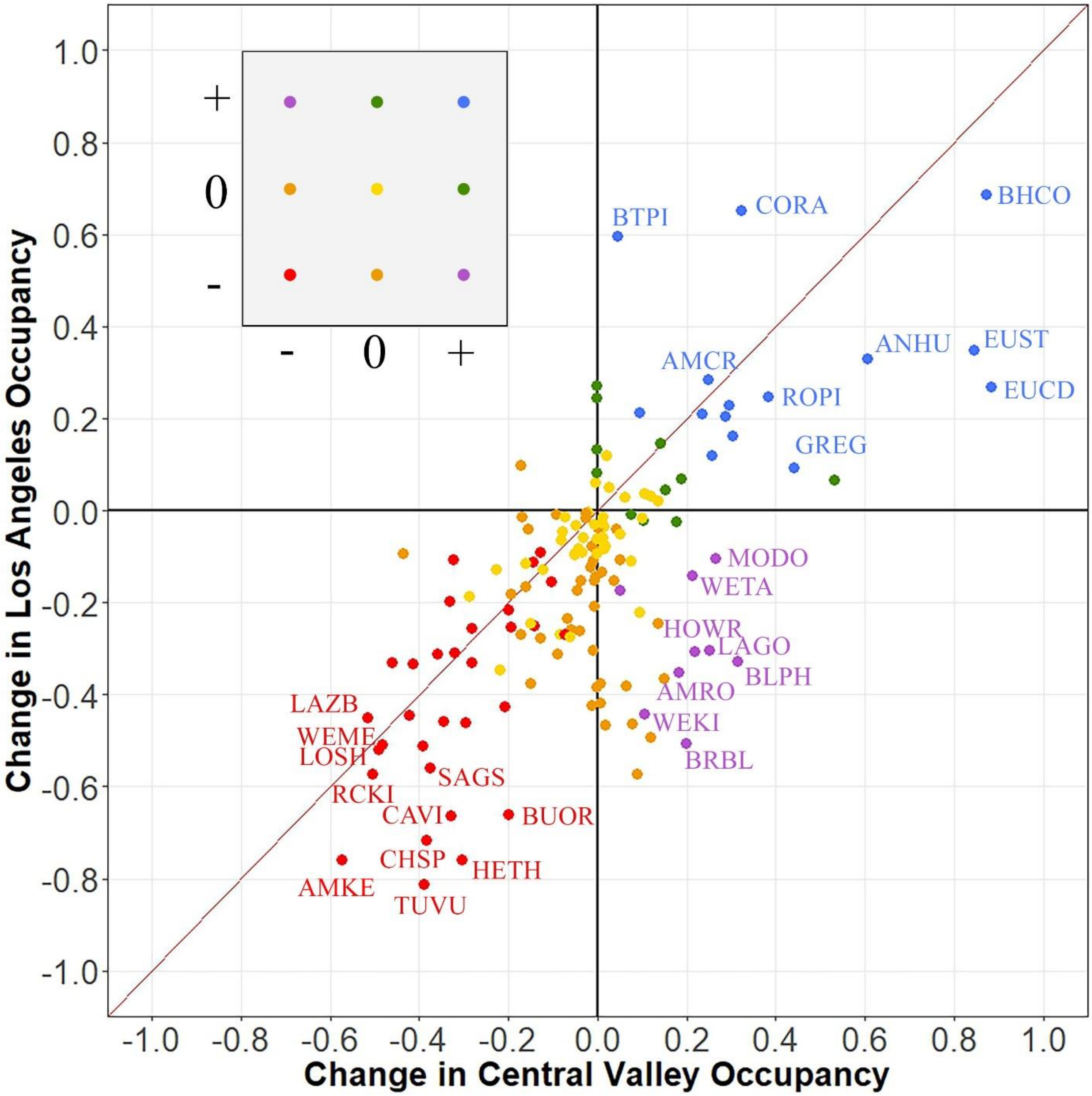

Figure 3: Species-specific change in occupancy at Los Angeles sites plotted against corresponding change in occupancy at Central Valley sites. Colors indicate whether changes were significantly positive, negative, or stable in one or both regions (e.g. blue = significant increase in both regions).

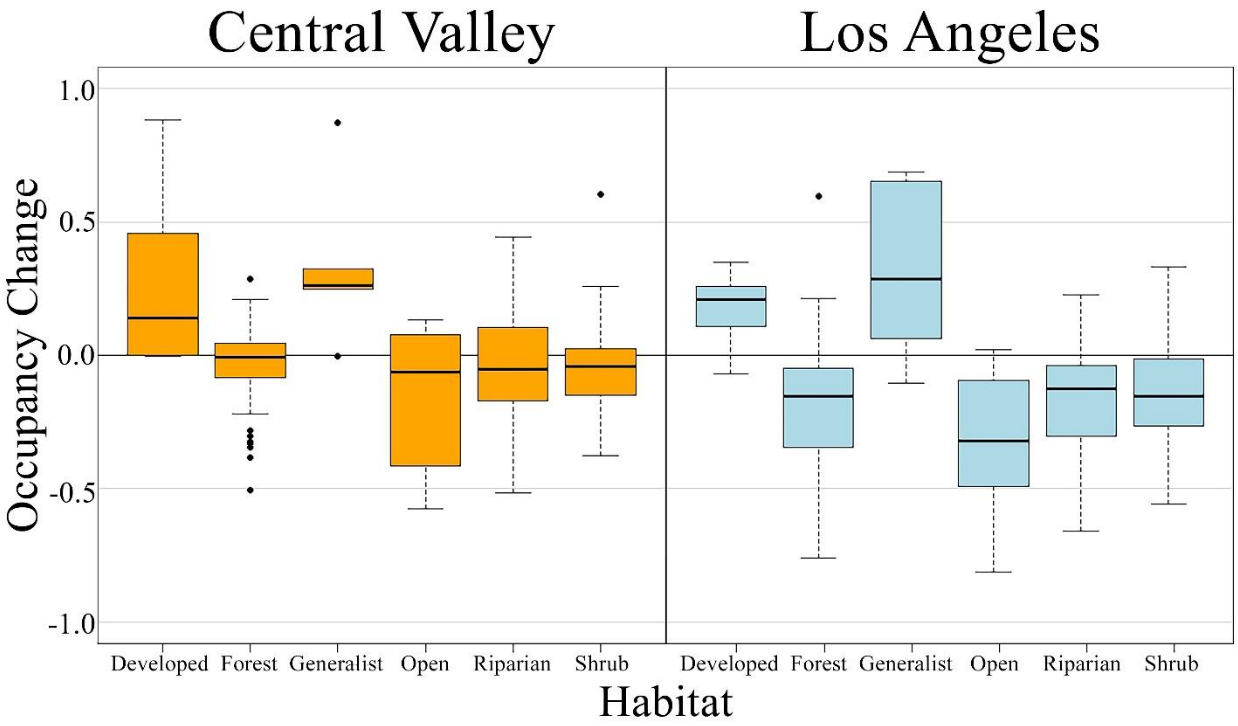

Figure 4: Changes in species-specific occupancy grouped by habitat preference.

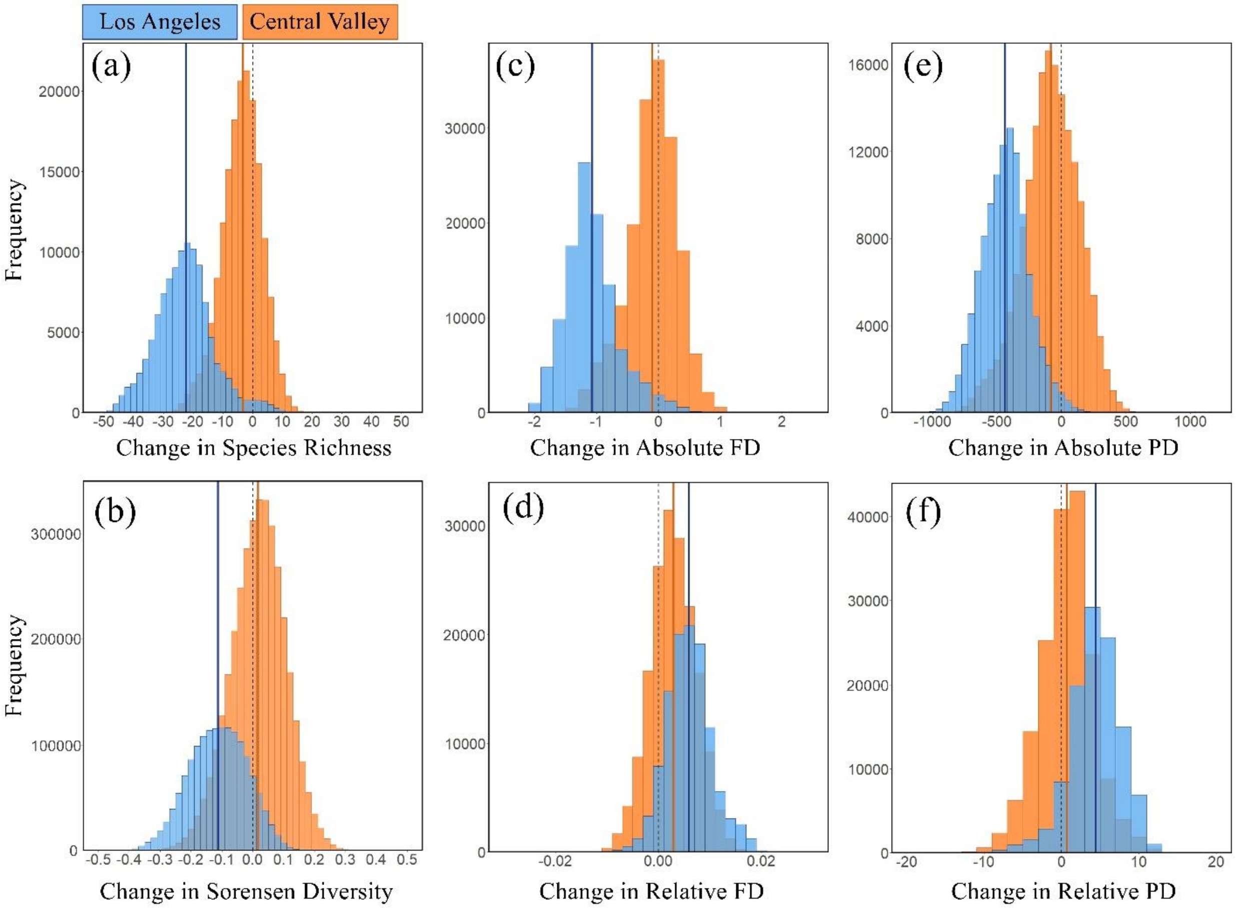

Figure 5: Posterior distributions for a century of change in (a) species richness per site, (b) Sorensen diversity between sites, (c) absolute functional diversity, (d) relative functional diversity, (e) absolute phylogenetic diversity, and (f) relative phylogenetic diversity. Colored lines indicate the mean of each distribution.

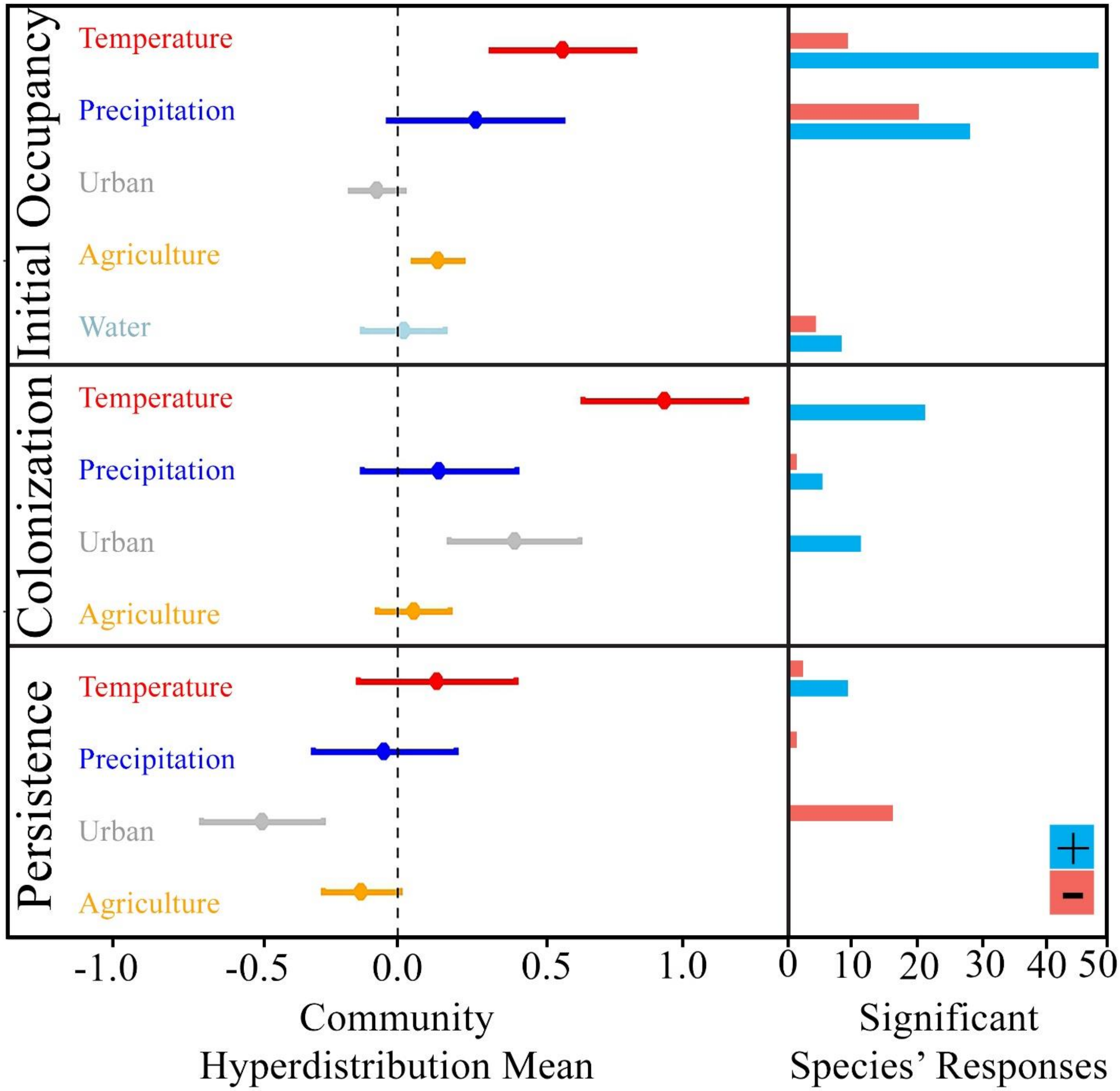

Figure 6: Coefficient values representing effects of covariates on initial occupancy probability, colonization probability, and persistence probability, summarized as the mean and 95% credible interval of the community-level hyperdistributions, and corresponding counts of individual species with significant positive or negative coefficient effects

Table S1: Traits for all species in our analysis: log-transformed body mass, body length, wingspan, migratory behavior (mig), territorial (ter), altricial (alt), mating behavior, breeding behavior, maximum lifespan, number of broods per year, mean clutch size, nest type, diet, foraging location, nest location, main habitat, human adapter. See Table S2 for guide to species 4-letter codes.

code	body mass (g)	body length (in)	wing span (in)	mig	terr	alt	mating	breed	lifespan (years)	brood per year	mean clutch size	nest type	diet	foraging	nest location	main habitat	human adapter
ACWO	4.14	9.25	16	resident	0	1	mono	Pair	12.1	1	4	cavity	omnivore	tree	tree	forest	0
ALHU	1.10	3.75	4.25	short	1	1	poly	Female	4	2	2	open	nectar	hover	shrub	shrub	0
AMCR	6.11	17.50	39	resident	0	1	mono	Coop	20	2	4.5	open	omnivore	ground	tree	generalist	1
AMGO	2.56	5.00	9	short	0	1	mono	Pair	13	2	4.5	open	seed	shrub	shrub	open	0
AMKE	4.76	9.00	22	resident	0	1	poly	Pair	9.8	1	4.5	cavity	invertebrate	hawk	tree	open	0
AMRO	4.34	10.00	17	resident	1	1	mono	Pair	17	3	4	open	omnivore	ground	shrub	forest	1
ANHU	1.46	4.00	5.25	resident	1	1	poly	Female	8.5	2	2	open	nectar	hover	shrub	shrub	1
ATFL	3.30	8.50	12	long	1	1	mono	Pair	11	1	4.5	cavity	invertebrate	hover	tree	shrub	0
BARS	2.94	6.75	15	long	0	1	poly	Occ	16	2	5	closed	invertebrate	aerial	rock	riparian_wetlands	0
BCHU	0.48	3.75	4.75	long	1	1	poly	Female	11.2	1	2	open	nectar	hover	shrub	shrub	0
BCNH	2.91	25.00	44	resident	0	0	mono	Pair	21.1	1	4	open	vertfishscav	aquatic	tree	riparian_wetlands	0
BCSP	2.48	5.75	7.75	short	0	1	mono	Pair	3	1	3.5	open	omnivore	ground	shrub	shrub	0
BEKI	5.01	13.00	20	short	1	1	mono	Pair	NA	1	7	cavity	vertfishscav	aquatic	ground	riparian_wetlands	0
BEVI	2.14	4.75	7	long	1	1	poly	Pair	7.1	2	4	open	invertebrate	shrub	shrub	riparian_wetlands	0
BEWR	2.30	5.25	7	resident	1	1	mono	Pair	8	3	6	cavity	invertebrate	ground	shrub	shrub	0
BGGN	1.79	4.50	6	short	1	1	mono	Pair	4.2	2	4.5	open	invertebrate	hover	tree	forest	0
BHCO	3.78	7.50	12	resident	0	1	poly	Parasite	16.9	NA	1	parasite	omnivore	ground	tree	generalist	1
BHGR	3.81	8.25	12.5	long	1	1	mono	Pair	11.9	1	3.5	open	omnivore	tree	shrub	riparian_wetlands	0
BLGR	1.51	6.75	11	long	1	1	mono	Pair	10.2	2	4	open	invertebrate	shrub	shrub	riparian_wetlands	0
BLPH	2.94	7.00	11	resident	1	1	mono	Pair	8	2	4.5	open	invertebrate	hover	rock	riparian_wetlands	1
BRBL	4.14	9.00	15.5	short	1	1	poly	Pair	12.5	2	5.5	open	omnivore	tree	tree	riparian_wetlands	1

BRCR	2.13	5.25	7.75	short	1	1	mono	Pair	4.6	1	5	cavity	invertebrate	bark	tree	forest	0
BRSP	2.35	5.50	7.5	short	1	1	mono	Occ	6.2	1	3.5	open	omnivore	shrub	shrub	shrub	0
BTPI	2.53	14.50	26	resident	0	1	mono	Pair	18.5	1	1	open	omnivore	tree	tree	forest	0
BTYW	2.13	5.00	7.75	long	0	1	mono	Pair	7	2	4	open	invertebrate	shrub	shrub	forest	0
BUOR	3.58	9.00	12	long	0	1	mono	Pair	8	1	4.5	closed	invertebrate	tree	tree	riparian_wetlands	0
BUOW	2.18	9.50	21	resident	1	0	mono	Pair	8	1	6.5	cavity	vertfishscav	hawk	ground	open	0
BUSH	1.67	4.50	6	resident	0	1	mono	Occ	8.4	2	4.5	closed	invertebrate	tree	tree	forest	0
CACW	3.66	8.50	11	resident	1	1	mono	Coop	6.3	2	4.5	closed	invertebrate	shrub	shrub	shrub	0
CAFI	3.26	6.25	11.5	short	1	1	mono	Pair	7	1	4.5	open	seed	tree	tree	forest	0
CAGN	1.61	4.50	5.5	resident	1	1	mono	Pair	8	3	3.8	open	invertebrate	shrub	shrub	shrub	0
CAHU	0.99	3.25	4.25	long	1	1	poly	Female	6.1	1	2	open	nectar	hover	tree	forest	0
CAKI	3.83	9.00	16	short	1	1	mono	Pair	NA	2	3.5	open	invertebrate	hover	tree	open	0
CALT	3.78	11.50	9	resident	1	1	mono	Pair	12.8	2	3	open	seed	ground	shrub	shrub	0
CANG	8.01	35.00	50	short	1	0	mono	Pair	24	1	5	open	vegetation	aquatic	ground	riparian_wetlands	1
CANW	2.35	5.75	7.5	resident	1	1	mono	Pair	NA	2	5.5	cavity	invertebrate	rock	rock	shrub	0
CAQU	5.19	10.00	14	resident	0	0	mono	Occ	9.6	2	15	open	seed	ground	ground	shrub	1
CATH	4.43	12.00	12.5	resident	1	1	mono	Pair	6.9	2	3	open	invertebrate	ground	shrub	shrub	0
CAVI	2.77	5.50	9.5	long	1	1	mono	Pair	NA	1	3.5	open	invertebrate	tree	tree	forest	0
CHSP	2.48	5.50	8.5	short	1	1	poly	Coop	11.8	2	4	open	seed	ground	shrub	forest	0
CLNU	4.87	12.00	24	resident	1	1	mono	Pair	17.4	1	3	open	omnivore	tree	tree	forest	0
CLSW	3.04	5.50	13.5	long	0	1	poly	Pair	12	1	4	closed	invertebrate	aerial	rock	open	1
COGD	3.40	6.50	10.5	resident	0	1	mono	Pair	7.2	4	2	open	seed	ground	tree	open	0
COHA	6.11	16.50	31	short	1	1	mono	Pair	12	1	4.5	open	vertfishscav	hawk	tree	forest	1
COHU	1.13	3.50	4.75	short	1	1	poly	Female	6	1	2	open	nectar	hover	shrub	shrub	0
CORA	7.09	24.00	53	resident	0	1	mono	Pair	21.9	1	5	open	omnivore	ground	tree	generalist	1
COYE	2.30	5.00	6.75	short	1	1	poly	Pair	11.5	2	4.5	open	invertebrate	shrub	shrub	riparian_wetlands	0
DEJU	2.94	6.25	9.25	short	1	1	mono	Pair	11.3	3	4	open	seed	ground	ground	forest	0
DOWO	3.30	6.75	12	resident	1	1	mono	Pair	11.9	1	4.8	cavity	invertebrate	tree	tree	forest	0

EUCD	5.30	13.00	22	resident	0	1	mono	Pair	17.8	4	3	open	seed	ground	rock	developed	1
EUST	4.41	8.50	16	resident	1	1	poly	Occ	22.9	3	6	cavity	omnivore	ground	tree	developed	1
GBHE	7.78	46.00	72	resident	0	1	mono	Pair	24.5	1	4.5	open	vertfishscav	aquatic	tree	riparian_wetlands	0
GOEA	8.43	30.00	79	short	1	1	mono	Pair	38	1	2	open	vertfishscav	hawk	tree	open	0
GREG	6.77	39.00	51	resident	0	1	mono	Pair	22.8	1	3.5	open	vertfishscav	aquatic	tree	riparian_wetlands	0
GRFL	2.53	6.00	8.75	long	1	1	poly	Pair	3.5	NA	3.5	open	invertebrate	hover	shrub	shrub	0
GRHE	5.35	18.00	26	resident	0	1	mono	Pair	11.6	1	3	open	vertfishscav	aquatic	tree	riparian_wetlands	0
GRRO	5.94	23.00	22	resident	1	1	mono	Pair	7	2	4	open	vertfishscav	ground	shrub	shrub	0
GTGR	5.25	18.00	23	resident	0	1	poly	Female	12.9	3	2.5	open	omnivore	ground	tree	developed	1
GTTO	3.37	7.25	9.75	short	1	1	mono	Pair	7.7	2	3	open	seed	ground	shrub	shrub	0
HAFL	2.30	5.50	8.75	long	1	1	mono	Pair	7	2	3.5	open	invertebrate	hover	tree	forest	0
HAWO	4.19	9.25	15	resident	1	1	mono	Pair	15.9	1	4	cavity	invertebrate	tree	tree	forest	0
HETH	3.43	6.75	11.5	short	1	1	mono	Pair	9.3	3	5	open	invertebrate	tree	ground	forest	0
HOFI	3.04	6.00	9.5	resident	0	1	mono	Pair	11.6	6	5	open	seed	ground	tree	developed	1
HOLA	3.47	7.25	12	resident	1	1	mono	Occ	8	3	3.5	open	omnivore	ground	ground	open	0
HOOR	3.18	8.00	10.5	long	1	1	mono	Pair	6	3	4	closed	omnivore	tree	tree	riparian_wetlands	0
HOSP	3.33	6.25	9.5	resident	0	1	mono	Coop	23	4	4.5	cavity	omnivore	ground	rock	developed	1
HOWR	2.40	4.75	6	short	1	1	mono	Occ	9	2	6	cavity	invertebrate	shrub	tree	riparian_wetlands	0
HUVI	2.40	5.00	8	resident	1	1	mono	Pair	6.5	1	4	open	invertebrate	tree	tree	forest	0
INPE	3.63	38.00	48	resident	0	0	poly	Female	25	1	6	open	omnivore	ground	ground	developed	1
KILL	4.55	10.50	24	resident	0	0	mono	Pair	12	2	4	open	invertebrate	ground	ground	open	1
LAGO	1.04	4.75	8.25	short	0	1	mono	Pair	5.7	1	4.5	open	seed	shrub	shrub	shrub	0
LASP	3.37	6.50	11	resident	1	1	poly	Pair	7.8	2	4.5	open	seed	ground	ground	open	0
LAZB	2.74	5.50	8.75	long	1	1	mono	Pair	9.9	2	4	open	omnivore	ground	shrub	riparian_wetlands	0
LCTH	4.13	11.00	12	resident	1	1	mono	Pair	5.7	NA	3	open	invertebrate	ground	shrub	shrub	0
LEGO	2.25	4.50	8	resident	0	1	mono	Pair	5.7	1	4	open	seed	ground	tree	generalist	1
LEWO	4.74	10.75	21	short	0	1	mono	Pair	NA	NA	6.5	cavity	seed	tree	tree	forest	0
LOSH	3.87	9.00	12	short	1	1	mono	Pair	12.5	2	5	open	vertfishscav	hover	shrub	open	0

MALL	7.00	23.00	35	resident	0	0	mono	Female	29.1	1	9	open	omnivore	aquatic	ground	riparian_wetlands	1
MAWR	2.40	5.00	6	short	1	1	poly	Pair	NA	3	5.5	closed	invertebrate	ground	shrub	riparian_wetlands	0
MGWA	2.35	5.25	7.5	long	1	1	mono	Pair	4.03	1	4	open	invertebrate	shrub	ground	forest	0
MOBL	3.37	7.25	14	short	1	1	mono	Occ	9	2	5	cavity	invertebrate	hover	rock	open	0
MOCH	2.40	5.25	8.5	resident	1	1	mono	Pair	10.1	2	8.5	cavity	omnivore	tree	tree	forest	0
MODO	5.01	11.50	18	resident	0	1	mono	Pair	31.3	2	2	open	seed	ground	tree	generalist	1
MOUQ	5.39	11.00	16	resident	0	0	mono	Pair	NA	NA	8.5	open	seed	ground	ground	forest	0
NAWA	2.16	4.75	7.5	long	1	1	mono	Pair	10.2	1	4.5	open	invertebrate	shrub	ground	forest	0
NOFL	4.87	12.50	20	short	1	1	mono	Pair	12.5	2	7.5	cavity	invertebrate	ground	tree	forest	0
NOHA	6.04	18.00	43	short	1	1	poly	Occ	17.1	1	4	open	vertfishscav	hawk	ground	riparian_wetlands	0
NOMO	3.89	10.00	14	resident	1	1	mono	Pair	8	3	4	open	omnivore	ground	shrub	developed	1
NRWS	2.77	5.50	14	long	0	1	mono	Pair	5.9	1	6.5	cavity	invertebrate	aerial	rock	riparian_wetlands	0
NUWO	3.64	7.50	13	resident	1	1	mono	Pair	7.8	NA	4.5	cavity	invertebrate	tree	tree	forest	0
OATI	2.83	5.75	9	resident	1	1	mono	Pair	8.8	2	7	cavity	omnivore	bark	tree	forest	0
OCWA	2.20	5.00	7.25	short	1	1	mono	Pair	8.5	2	4.5	open	invertebrate	aerial	ground	forest	0
OSFL	3.47	7.50	13	long	1	1	mono	Pair	7.1	2	3.5	open	invertebrate	hover	tree	forest	0
PHAI	3.18	7.75	11	short	1	1	mono	Pair	NA	3	2.5	open	fruit	tree	shrub	shrub	0
PIJA	4.61	10.50	19	resident	0	1	mono	Coop	11	NA	4.5	open	omnivore	tree	tree	forest	0
PISI	2.71	5.00	9	short	0	1	mono	Pair	9.4	1	3.5	open	seed	tree	tree	forest	0
PSFL	2.40	5.50	8	long	1	1	poly	Pair	6.9	2	4	open	invertebrate	hover	tree	forest	0
PUFI	3.22	6.00	10	short	1	1	mono	Pair	14	1	5	open	seed	tree	tree	forest	0
PUMA	4.03	8.00	18	long	0	1	mono	Pair	13.8	1	5	cavity	invertebrate	aerial	rock	riparian_wetlands	0
PYNU	2.35	4.25	7.75	resident	0	1	mono	Coop	8.2	1	7.5	cavity	seed	bark	tree	forest	0
RBNU	3.04	5.75	11	short	1	1	mono	Pair	9.8	1	7	cavity	seed	bark	tree	forest	0
RBSA	3.91	8.50	16	short	1	1	mono	Pair	4.8	NA	5.5	cavity	invertebrate	tree	tree	forest	0
RCKI	1.87	4.25	7.5	short	1	1	mono	Pair	5.6	1	7.5	open	invertebrate	tree	tree	forest	0
RCPA	2.50	12.00	25	resident	0	1	mono	Pair	60	1	3	cavity	fruit	tree	tree	developed	1
RCSP	2.92	6.00	7.75	resident	1	1	mono	Pair	3.2	2	3	open	seed	ground	ground	shrub	0
RNEP	7.05	35.00	31	resident	1	0	poly	Female	3	1	11	open	vegetation	ground	ground	open	0

ROPI	5.60	12.50	28	resident	0	1	mono	Pair	6	5	2	open	seed	ground	rock	developed	1
ROWR	2.80	6.00	9	resident	1	1	mono	Pair	NA	3	5.5	cavity	invertebrate	rock	rock	shrub	0
RSHA	6.45	17.00	40	resident	1	1	mono	Occ	20	1	3.5	open	vertfishscav	hawk	tree	forest	0
RTHA	6.98	19.00	49	resident	1	1	mono	Pair	29.5	1	3	open	vertfishscav	hawk	tree	open	0
RWBL	3.95	8.75	13	resident	1	1	poly	Pair	20	3	5	open	omnivore	shrub	shrub	riparian_wetlands	0
RWBU	1.46	7.90	11	resident	1	1	mono	Pair	11	2	2.5	open	fruit	tree	shrub	developed	1
SAGS	2.80	6.00	8.25	resident	1	1	mono	Pair	NA	3	3.5	open	invertebrate	ground	ground	shrub	0
SAPH	3.04	7.50	13	short	1	1	mono	Pair	NA	2	4.5	cavity	invertebrate	hover	rock	shrub	0
SAVS	3.00	5.50	6.75	short	1	1	mono	Pair	6.8	2	3	open	invertebrate	ground	ground	open	0
SNEG	5.89	24.00	41	short	0	1	mono	Pair	22.8	1	4.5	open	vertfishscav	aquatic	tree	riparian_wetlands	0
SOSP	3.00	6.25	8.25	resident	1	1	poly	Pair	11.3	2	4	open	seed	ground	ground	riparian_wetlands	0
SPTO	3.69	8.50	10.5	resident	1	1	mono	Pair	10.7	2	4	open	seed	ground	ground	shrub	0
SSHA	4.94	11.00	23	short	1	1	mono	Female	19.9	1	4.5	open	vertfishscav	hawk	tree	forest	1
STJA	4.65	11.50	19	resident	1	1	mono	Pair	16.1	1	4	open	omnivore	tree	tree	forest	0
SWHA	6.75	19.00	51	long	1	1	mono	Pair	19.6	1	2.5	open	vertfishscav	hawk	tree	open	0
SWTH	3.43	7.00	12	long	1	1	mono	Pair	11	2	3.5	open	invertebrate	tree	shrub	forest	0
TOSO	3.53	8.50	14.5	short	0	1	mono	Pair	NA	2	4	open	invertebrate	hover	ground	forest	0
TRBL	4.08	8.75	14	resident	0	1	poly	Pair	13.2	2	2.5	open	invertebrate	shrub	shrub	riparian_wetlands	0
TRES	3.00	5.75	14.5	short	0	1	poly	Pair	12.1	1	5.5	cavity	invertebrate	aerial	tree	riparian_wetlands	0
TUVU	7.51	26.00	67	short	0	1	mono	Pair	17	1	2	cavity	vertfishscav	ground	rock	open	0
VASW	1.27	4.75	12	long	0	1	mono	Pair	5	1	6	cavity	invertebrate	aerial	tree	forest	0
VESP	3.26	6.25	10	short	1	1	mono	Pair	7.9	2	4	open	seed	ground	ground	open	0
VGSW	2.64	5.25	13.5	short	0	1	mono	Occ	6.8	1	4.5	cavity	invertebrate	aerial	tree	riparian_wetlands	0
WAVI	2.48	5.50	8.5	long	1	1	mono	Pair	13	2	4	open	invertebrate	tree	tree	forest	0
WBNU	2.30	4.50	8.5	resident	1	1	mono	Pair	7.5	1	6	cavity	seed	bark	tree	forest	0
WEBL	3.37	7.00	13.5	short	1	1	mono	Coop	6	2	5	cavity	invertebrate	hover	tree	open	0
WEKI	3.69	8.75	15.5	long	1	1	mono	Pair	6.9	2	4	open	invertebrate	hover	tree	open	1
WEME	4.57	9.50	14.5	resident	1	1	poly	Pair	10	2	5	open	invertebrate	ground	ground	open	0

WESJ	4.44	11.50	15.5	resident	1	1	mono	Occ	15.8	1	5	open	omnivore	shrub	shrub	shrub	1
WETA	3.33	7.25	11.5	long	1	1	mono	Pair	15.3	1	4	open	omnivore	tree	tree	forest	0
WEWP	2.56	6.25	10.5	long	1	1	mono	Pair	7	1	3	open	invertebrate	hover	tree	forest	0
WHWO	4.11	9.25	16	resident	1	1	mono	Pair	NA	1	4.5	cavity	omnivore	tree	tree	forest	0
WIFL	2.60	5.75	8.5	long	1	1	poly	Pair	11	2	3.5	open	invertebrate	hover	shrub	riparian_wetlands	0
WITU	8.91	46.00	64	resident	0	0	poly	Female	13	1	11.5	open	omnivore	ground	ground	forest	0
WIWA	2.04	4.75	7	long	1	1	poly	Pair	6.8	1	4.5	open	invertebrate	shrub	shrub	riparian_wetlands	1
WREN	2.64	6.50	7	resident	1	1	mono	Pair	12.6	2	4	closed	omnivore	shrub	tree	shrub	0
WTSW	3.47	6.50	15	long	0	1	mono	Pair	10	NA	4.5	cavity	invertebrate	aerial	rock	forest	0
YBCH	3.22	7.50	9.75	long	1	1	poly	Pair	8.9	2	4.5	open	invertebrate	shrub	shrub	riparian_wetlands	0
YBMA	5.04	16.50	24	resident	0	1	mono	Pair	10	NA	6.5	open	omnivore	ground	tree	open	0
YCPA	1.79	8.75	15	resident	0	1	mono	Pair	19	1	5	c	fruit	tree	tree	developed	1
YEWA	2.25	5.00	1	long	1	1	poly	Pair	10	1	4.5	open	invertebrate	shrub	tree	riparian_wetlands	0
YHBL	4.17	9.50	15	short	0	1	poly	Pair	18	2	4	closed	omnivore	ground	ground	riparian_wetlands	0

Table S2: Species-specific probability of initial occupancy, change in occupancy probability, survival probability, and colonization probability. Values are Mean ± 1SD.

species	code	initial occupancy	occupancy change	survival	colonization
Melanerpes carolinus	ACWO	0.59 ± 0.03	0 ± 0.03	0.95 ± 0.13	0.04 ± 0.05
Selasphorus sasin	ALHU	0.28 ± 0.06	-0.06 ± 0.06	0.3 ± 0.16	0.06 ± 0.04
Corvus brachyrhynchos	AMCR	0.21 ± 0.02	0.26 ± 0.02	0.65 ± 0.09	0.47 ± 0.08
Spinus tristis	AMGO	0.55 ± 0.05	-0.38 ± 0.06	0.2 ± 0.05	0.07 ± 0.07
Falco sparverius	AMKE	0.82 ± 0.05	-0.65 ± 0.06	0.1 ± 0.09	0.36 ± 0.21
Turdus migratorius	AMRO	0.6 ± 0.07	-0.03 ± 0.07	0.56 ± 0.03	0.49 ± 0.15
Calypte anna	ANHU	0.36 ± 0.02	0.49 ± 0.02	0.96 ± 0.06	0.82 ± 0.06
Myiarchus cinerascens	ATFL	0.91 ± 0.04	-0.18 ± 0.04	0.8 ± 0.13	0.15 ± 0.24
Hirundo rustica	BARS	0.51 ± 0.1	-0.18 ± 0.1	0.49 ± 0.17	0.11 ± 0.1
Archilochus alexandri	BCHU	0.31 ± 0.07	-0.05 ± 0.1	0.21 ± 0.17	0.17 ± 0.11
Nycticorax nycticorax	BCNH	0.39 ± 0.07	-0.12 ± 0.08	0.62 ± 0.13	0.01 ± 0.03
Spizella atrogularis	BCSP	0.31 ± 0.05	-0.18 ± 0.05	0.23 ± 0.18	0 ± 0
Megaceryle alcyon	BEKI	0.34 ± 0.08	-0.15 ± 0.08	0.62 ± 0.06	0.01 ± 0.01
Vireo bellii	BEVI	0.3 ± 0.04	-0.27 ± 0.04	0.09 ± 0.04	0 ± 0
Thryomanes bewickii	BEWR	0.68 ± 0.05	0.06 ± 0.05	0.91 ± 0.09	0.32 ± 0.17
Polioptila caerulea	BGGN	0.57 ± 0.03	-0.3 ± 0.03	0.44 ± 0.21	0.02 ± 0.02
Molothrus ater	BHCO	0.03 ± 0.01	0.79 ± 0.01	0.76 ± 0.07	0.85 ± 0.04
Pheucticus melanocephalus	BHGR	0.67 ± 0.04	-0.13 ± 0.04	0.75 ± 0.15	0.13 ± 0.1
Passerina caerulea	BLGR	0.31 ± 0.06	-0.14 ± 0.06	0.4 ± 0.08	0.05 ± 0.04
Sayornis nigricans	BLPH	0.67 ± 0.04	0.05 ± 0.04	0.76 ± 0.1	0.71 ± 0.14
Euphagus cyanocephalus	BRBL	0.67 ± 0.05	-0.08 ± 0.05	0.51 ± 0.25	0.75 ± 0.13
Certhia americana	BRCR	0.11 ± 0.03	-0.04 ± 0.03	0.54 ± 0.16	0.01 ± 0.01
Spizella breweri	BRSP	0.25 ± 0.07	-0.21 ± 0.07	0.14 ± 0.21	0 ± 0.01
Patagioenas fasciata	BTPI	0.04 ± 0.02	0.26 ± 0.02	0.77 ± 0.18	0.18 ± 0.06
Setophaga nigrescens	BTYW	0.36 ± 0.03	-0.13 ± 0.04	0.51 ± 0.09	0.02 ± 0.03
Icterus bullockii	BUOR	0.88 ± 0.04	-0.38 ± 0.04	0.42 ± 0.09	0.37 ± 0.28
Athene cunicularia	BUOW	0.31 ± 0.07	-0.29 ± 0.08	0.06 ± 0.03	0 ± 0.02
Psaltriparus minimus	BUSH	0.76 ± 0.05	0 ± 0.05	0.91 ± 0.22	0.19 ± 0.17
Campylorhynchus brunneicapillus	CACW	0.04 ± 0.02	-0.03 ± 0.02	0.24 ± 0.27	0 ± 0
Carpodacus cassinii	CAFI	0.06 ± 0.01	-0.03 ± 0.01	0.47 ± 0.2	0 ± 0
Polioptila californica	CAGN	0.05 ± 0.01	-0.05 ± 0.02	0.22 ± 0.22	0 ± 0
Stellula calliope	CAHU	0.17 ± 0.02	-0.15 ± 0.02	0.3 ± 0.21	0 ± 0
Tyrannus vociferans	CAKI	0.07 ± 0.03	-0.06 ± 0.03	0.23 ± 0.04	0 ± 0
Melozone crissalis	CALT	0.67 ± 0.02	0.05 ± 0.02	0.88 ± 0.24	0.36 ± 0.14
Branta canadensis	CANG	0.05 ± 0.04	0.26 ± 0.04	0.71 ± 0.14	0.2 ± 0.06
Catherpes mexicanus	CANW	0.22 ± 0.01	-0.11 ± 0.01	0.34 ± 0.03	0 ± 0

Callipepla californica	CAQU	0.63 ± 0.02	-0.04 ± 0.02	0.95 ± 0.11	0.05 ± 0.06
Toxostoma redivivum	CATH	0.51 ± 0.04	-0.21 ± 0.05	0.42 ± 0.05	0.05 ± 0.04
Vireo cassinii	CAVI	0.54 ± 0.06	-0.46 ± 0.06	0.1 ± 0.04	0.01 ± 0.02
Spizella passerina	CHSP	0.6 ± 0.03	-0.51 ± 0.03	0.11 ± 0.28	0 ± 0.01
Nucifraga columbiana	CLNU	0.07 ± 0.02	-0.02 ± 0.02	0.5 ± 0.09	0 ± 0
Petrochelidon pyrrhonota	CLSW	0.69 ± 0.07	-0.13 ± 0.07	0.7 ± 0.26	0.25 ± 0.16
Columbina passerina	COGD	0.02 ± 0.04	0.05 ± 0.06	NA	0.03 ± 0.05
Accipiter cooperii	COHA	0.46 ± 0.17	-0.01 ± 0.19	0.58 ± 0.15	0.28 ± 0.23
Calypte costae	COHU	0.26 ± 0.05	-0.14 ± 0.05	0.29 ± 0.06	0.03 ± 0.03
Corvus corax	CORA	0.37 ± 0.1	0.45 ± 0.1	0.92 ± 0.11	0.79 ± 0.09
Geothlypis trichas	COYE	0.47 ± 0.04	-0.27 ± 0.04	0.38 ± 0.11	0.01 ± 0.02
Junco hyemalis	DEJU	0.57 ± 0.05	-0.23 ± 0.05	0.42 ± 0.08	0.05 ± 0.05
Picoides pubescens	DOWO	0.42 ± 0.1	-0.24 ± 0.11	0.08 ± 0.18	0.16 ± 0.12
Streptopelia decaocto	EUCD	NA	0.63 ± 0.01	NA	0.66 ± 0.07
Sturnus vulgaris	EUST	0.06 ± 0.04	0.64 ± 0.04	0.79 ± 0.13	0.74 ± 0.07
Ardea herodias	GBHE	0.39 ± 0.06	-0.06 ± 0.06	0.77 ± 0.22	0.03 ± 0.03
Aquila chrysaetos	GOEA	0.33 ± 0.16	-0.16 ± 0.18	0.25 ± 0.27	0.08 ± 0.13
Ardea alba	GREG	0.04 ± 0.04	0.29 ± 0.04	0.68 ± 0.18	0.21 ± 0.07
Empidonax wrightii	GRFL	0.2 ± 0.04	-0.18 ± 0.04	0.2 ± 0.25	0 ± 0.01
Butorides virescens	GRHE	0.1 ± 0.05	0.07 ± 0.05	0.65 ± 0.24	0.07 ± 0.04
Geococcyx californianus	GRRO	0.4 ± 0.09	-0.24 ± 0.12	0.38 ± 0.24	0.01 ± 0.03
Quiscalus mexicanus	GTGR	NA	0.14 ± 0.06	NA	0.09 ± 0.05
Pipilo chlorurus	GTTO	0.1 ± 0	-0.01 ± 0	0.57 ± 0.18	0 ± 0
Empidonax hammondii	HAFL	0.18 ± 0.09	-0.15 ± 0.09	0.13 ± 0.14	0 ± 0.02
Picoides villosus	HAWO	0.28 ± 0.02	-0.15 ± 0.03	0.27 ± 0.08	0 ± 0
Catharus guttatus	HETH	0.51 ± 0.08	-0.48 ± 0.09	0.04 ± 0.02	0.01 ± 0.03
Carpodacus mexicanus	HOFI	0.9 ± 0.03	-0.02 ± 0.03	0.96 ± 0.09	0.51 ± 0.3
Eremophila alpestris	HOLA	0.55 ± 0.03	-0.36 ± 0.03	0.27 ± 0.21	0 ± 0.01
Icterus cucullatus	HOOR	0.22 ± 0.03	-0.03 ± 0.04	0.7 ± 0.14	0.01 ± 0.02
Passer domesticus	HOSP	0.29 ± 0.05	0.22 ± 0.05	0.76 ± 0.09	0.33 ± 0.09
Troglodytes aedon	HOWR	0.49 ± 0.02	0 ± 0.02	0.6 ± 0.12	0.26 ± 0.1
Vireo huttoni	HUVI	0.24 ± 0.02	-0.06 ± 0.03	0.82 ± 0.08	0 ± 0
Pavo cristatus	INPE	NA	0.03 ± 0.01	NA	0.01 ± 0.01
Charadrius vociferus	KILL	0.6 ± 0.06	0 ± 0.06	0.84 ± 0.16	0.25 ± 0.14
Spinus lawrencei	LAGO	0.44 ± 0.05	0.02 ± 0.07	0.53 ± 0.08	0.34 ± 0.12
Chondestes grammacus	LASP	0.74 ± 0.04	-0.44 ± 0.04	0.26 ± 0.07	0.06 ± 0.08
Passerina amoena	LAZB	0.66 ± 0.07	-0.48 ± 0.07	0.16 ± 0.17	0.01 ± 0.03
Toxostoma lecontei	LCTH	0.06 ± 0.02	-0.05 ± 0.02	0.17 ± 0.04	0 ± 0
Spinus psaltria	LEGO	0.71 ± 0.06	0.02 ± 0.06	0.88 ± 0.14	0.31 ± 0.21
Melanerpes lewis	LEWO	0.13 ± 0.04	-0.12 ± 0.04	0.11 ± 0.07	0 ± 0.01
Lanius ludovicianus	LOSH	0.64 ± 0.04	-0.5 ± 0.04	0.21 ± 0.06	0.01 ± 0.02
Anas platyrhynchos	MALL	0.26 ± 0.06	0.24 ± 0.06	0.93 ± 0.2	0.25 ± 0.09
Cistothorus palustris	MAWR	0.07 ± 0.02	0 ± 0.02	0.71 ± 0.25	0.01 ± 0.01

Geothlypis tolmiei	MGWA	0.45 ± 0.17	-0.27 ± 0.19	0.3 ± 0.2	0.04 ± 0.12
Sialia currucoides	MOBL	0.08 ± 0.06	-0.06 ± 0.05	0.17 ± 0.16	0 ± 0.03
Poecile gambeli	MOCH	0.18 ± 0	-0.01 ± 0	0.8 ± 0.02	0 ± 0
Zenaida macroura	MODO	0.78 ± 0.04	0.11 ± 0.04	0.95 ± 0.19	0.79 ± 0.15
Oreortyx pictus	MOUQ	0.23 ± 0.01	-0.06 ± 0.01	0.66 ± 0.29	0 ± 0
Oreothlypis ruficapilla	NAWA	0.34 ± 0.16	-0.03 ± 0.22	0.36 ± 0.08	0.24 ± 0.24
Colaptes auratus	NOFL	0.77 ± 0.02	-0.39 ± 0.02	0.46 ± 0.21	0.02 ± 0.04
Circus cyaneus	NOHA	0.17 ± 0.07	-0.06 ± 0.07	0.47 ± 0.06	0.02 ± 0.02
Mimus polyglottos	NOMO	0.29 ± 0.03	0.34 ± 0.03	0.92 ± 0.11	0.54 ± 0.1
Stelgidopteryx serripennis	NRWS	0.39 ± 0.1	0.04 ± 0.1	0.76 ± 0.03	0.23 ± 0.12
Picoides nuttallii	NUWO	0.55 ± 0.05	0.14 ± 0.05	0.95 ± 0.04	0.34 ± 0.13
Baeolophus inornatus	OATI	0.4 ± 0.02	0.14 ± 0.02	0.93 ± 0.19	0.24 ± 0.07
Oreothlypis celata	OCWA	0.38 ± 0.05	-0.14 ± 0.07	0.41 ± 0.17	0.09 ± 0.06
Contopus cooperi	OSFL	0.31 ± 0.04	-0.11 ± 0.05	0.26 ± 0.13	0.04 ± 0.03
Phainopepla nitens	PHAI	0.42 ± 0.08	-0.18 ± 0.08	0.55 ± 0.29	0.05 ± 0.05
Gymnorhinus cyanocephalus	PIJA	0.05 ± 0.03	-0.02 ± 0.03	0.51 ± 0.25	0 ± 0.01
Spinus pinus	PISI	0.13 ± 0.04	-0.09 ± 0.04	0.26 ± 0.14	0 ± 0.01
Empidonax difficilis	PSFL	0.36 ± 0.04	-0.04 ± 0.04	0.65 ± 0.18	0.06 ± 0.05
Carpodacus purpureus	PUFI	0.31 ± 0.05	-0.13 ± 0.05	0.41 ± 0.15	0 ± 0.01
Progne subis	PUMA	0.21 ± 0.09	-0.18 ± 0.09	0.1 ± 0.21	0 ± 0.02
Sitta pygmaea	PYNU	0.14 ± 0.02	-0.04 ± 0.02	0.63 ± 0.28	0 ± 0
Sitta carolinensis	RBNU	0.07 ± 0.03	-0.02 ± 0.04	0.49 ± 0.21	0.01 ± 0.01
Sphyrapicus ruber	RBSA	0.13 ± 0.02	-0.05 ± 0.02	0.31 ± 0.09	0 ± 0
Regulus calendula	RCKI	0.65 ± 0.08	-0.53 ± 0.09	0.1 ± 0.28	0.02 ± 0.05
Amazona viridigenalis	RCPA	NA	0.1 ± 0.01	NA	0.04 ± 0.02
Aimophila ruficeps	RCSP	0.33 ± 0.16	-0.14 ± 0.16	0.41 ± 0.2	0.06 ± 0.12
Phasianus colchicus	RNEP	NA	0.04 ± 0.02	NA	0.03 ± 0.02
Columba livia	ROPI	NA	0.32 ± 0.04	NA	0.28 ± 0.07
Salpinctes obsoletus	ROWR	0.13 ± 0.02	-0.04 ± 0.03	0.62 ± 0.26	0 ± 0
Buteo lineatus	RSHA	0.05 ± 0.04	0.25 ± 0.05	0.49 ± 0.07	0.26 ± 0.06
Buteo jamaicensis	RTHA	0.7 ± 0.1	0.08 ± 0.1	0.84 ± 0.12	0.79 ± 0.2
Agelaius phoeniceus	RWBL	0.46 ± 0.03	-0.02 ± 0.03	0.7 ± 0.03	0.22 ± 0.09
Pycnonotus jocosus	RWBU	NA	0.05 ± 0.01	NA	0.01 ± 0.01
Amphispiza belli	SAGS	0.46 ± 0.07	-0.45 ± 0.07	0.04 ± 0.14	0 ± 0
Sayornis saya	SAPH	0.22 ± 0.04	-0.1 ± 0.04	0.34 ± 0.06	0.02 ± 0.02
Passerculus sandwichensis	SAVS	0.49 ± 0.08	-0.4 ± 0.08	0.09 ± 0.28	0.04 ± 0.05
Egretta thula	SNEG	0.04 ± 0.04	0.1 ± 0.04	0.33 ± 0.08	0.07 ± 0.03
Melospiza melodia	SOSP	0.58 ± 0.03	-0.2 ± 0.03	0.54 ± 0.02	0.13 ± 0.08
Pipilo maculatus	SPTO	0.68 ± 0.02	0.03 ± 0.02	0.95 ± 0.26	0.13 ± 0.09
Accipiter striatus	SSHA	0.4 ± 0.11	-0.18 ± 0.17	0.3 ± 0.12	0.14 ± 0.19
Cyanocitta stelleri	STJA	0.28 ± 0.02	-0.01 ± 0.02	0.84 ± 0.12	0.01 ± 0.01
Buteo swainsoni	SWHA	0.54 ± 0.07	-0.31 ± 0.08	0.28 ± 0.28	0.06 ± 0.07
Catharus ustulatus	SWTH	0.32 ± 0.14	-0.18 ± 0.15	0.33 ± 0.26	0.04 ± 0.09

Myadestes townsendi	TOSO	0.12 ± 0.03	-0.08 ± 0.04	0.37 ± 0.22	0 ± 0
Agelaius tricolor	TRBL	0.28 ± 0.06	-0.07 ± 0.06	0.52 ± 0.16	0.01 ± 0.02
Tachycineta bicolor	TRES	0.3 ± 0.04	-0.01 ± 0.04	0.63 ± 0.07	0.06 ± 0.04
Cathartes aura	TUVU	0.92 ± 0.04	-0.56 ± 0.04	0.29 ± 0.31	0.1 ± 0.17
Chaetura vauxi	VASW	0.27 ± 0.17	0.08 ± 0.22	0.45 ± 0.21	0.26 ± 0.25
Pooecetes gramineus	VESP	0.05 ± 0.03	-0.04 ± 0.03	0.21 ± 0.1	0 ± 0
Tachycineta thalassina	VGSW	0.45 ± 0.04	-0.18 ± 0.04	0.24 ± 0.13	0.14 ± 0.08
Vireo gilvus	WAVI	0.56 ± 0.05	-0.29 ± 0.08	0.34 ± 0.1	0.09 ± 0.08
Sitta canadensis	WBNU	0.41 ± 0.05	0 ± 0.05	0.8 ± 0.07	0.08 ± 0.05
Sialia mexicana	WEBL	0.52 ± 0.03	-0.01 ± 0.03	0.84 ± 0.08	0.13 ± 0.07
Tyrannus verticalis	WEKI	0.73 ± 0.03	-0.11 ± 0.03	0.78 ± 0.07	0.42 ± 0.19
Sturnella neglecta	WEME	0.79 ± 0.02	-0.49 ± 0.03	0.21 ± 0.01	0.22 ± 0.17
Aphelocoma californica	WESJ	0.58 ± 0.03	0.2 ± 0.03	0.97 ± 0.17	0.47 ± 0.12
Piranga ludoviciana	WETA	0.31 ± 0.03	0.06 ± 0.04	0.67 ± 0.1	0.19 ± 0.08
Contopus sordidulus	WEWP	0.52 ± 0.04	-0.08 ± 0.04	0.62 ± 0.25	0.11 ± 0.06
Picoides albolarvatus	WHWO	0.07 ± 0.01	-0.02 ± 0.01	0.48 ± 0.2	0 ± 0
Empidonax traillii	WIFL	0.23 ± 0.06	-0.16 ± 0.07	0.21 ± 0.1	0.01 ± 0.02
Meleagris gallopavo	WITU	NA	0.09 ± 0.06	NA	0.07 ± 0.04
Cardellina pusilla	WIWA	0.55 ± 0.11	-0.01 ± 0.11	0.79 ± 0.11	0.25 ± 0.17
Chamaea fasciata	WREN	0.42 ± 0.01	-0.13 ± 0.01	0.62 ± 0.15	0.01 ± 0.01
Aeronautes saxatalis	WTSW	0.23 ± 0.03	-0.05 ± 0.03	0.33 ± 0.07	0.07 ± 0.04
Icteria virens	YBCH	0.47 ± 0.06	-0.43 ± 0.07	0.07 ± 0.22	0.01 ± 0.02
Pica nuttalli	YBMA	0.11 ± 0.02	0 ± 0.03	0.45 ± 0.08	0.03 ± 0.02
Brotogeris chiriri	YCPA	NA	0.09 ± 0.01	NA	0.02 ± 0.02
Setophaga petechia	YEWA	0.78 ± 0.05	-0.34 ± 0.05	0.53 ± 0.19	0.07 ± 0.09
Xanthocephalus xanthocephalus	YHBL	0.15 ± 0.05	-0.1 ± 0.05	0.27 ± 0.38	0 ± 0.01

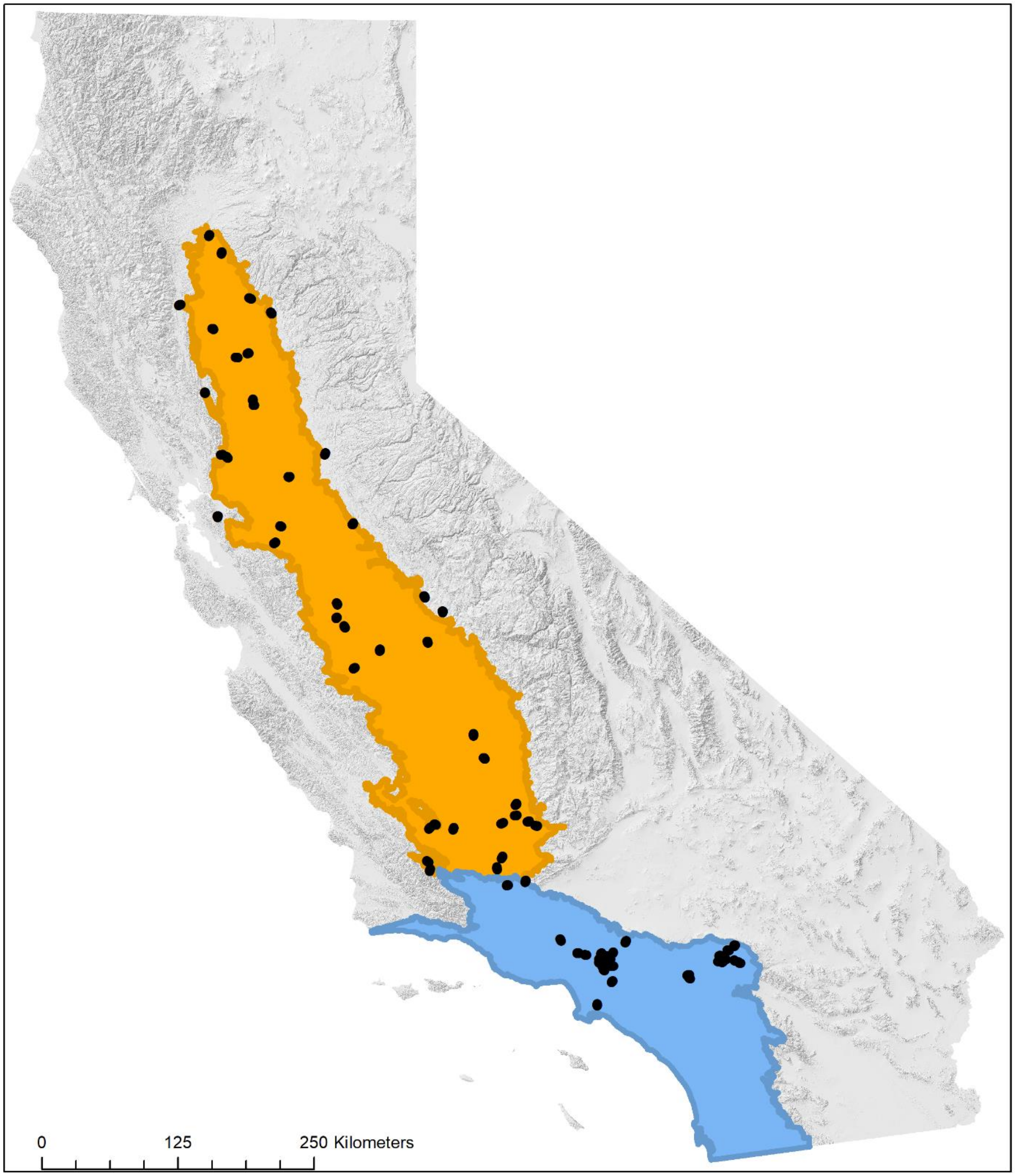

Figure S1: Map of survey locations. Colored areas indicate the extent of the Central Valley (orange) and Los Angeles (blue) ecoregions.

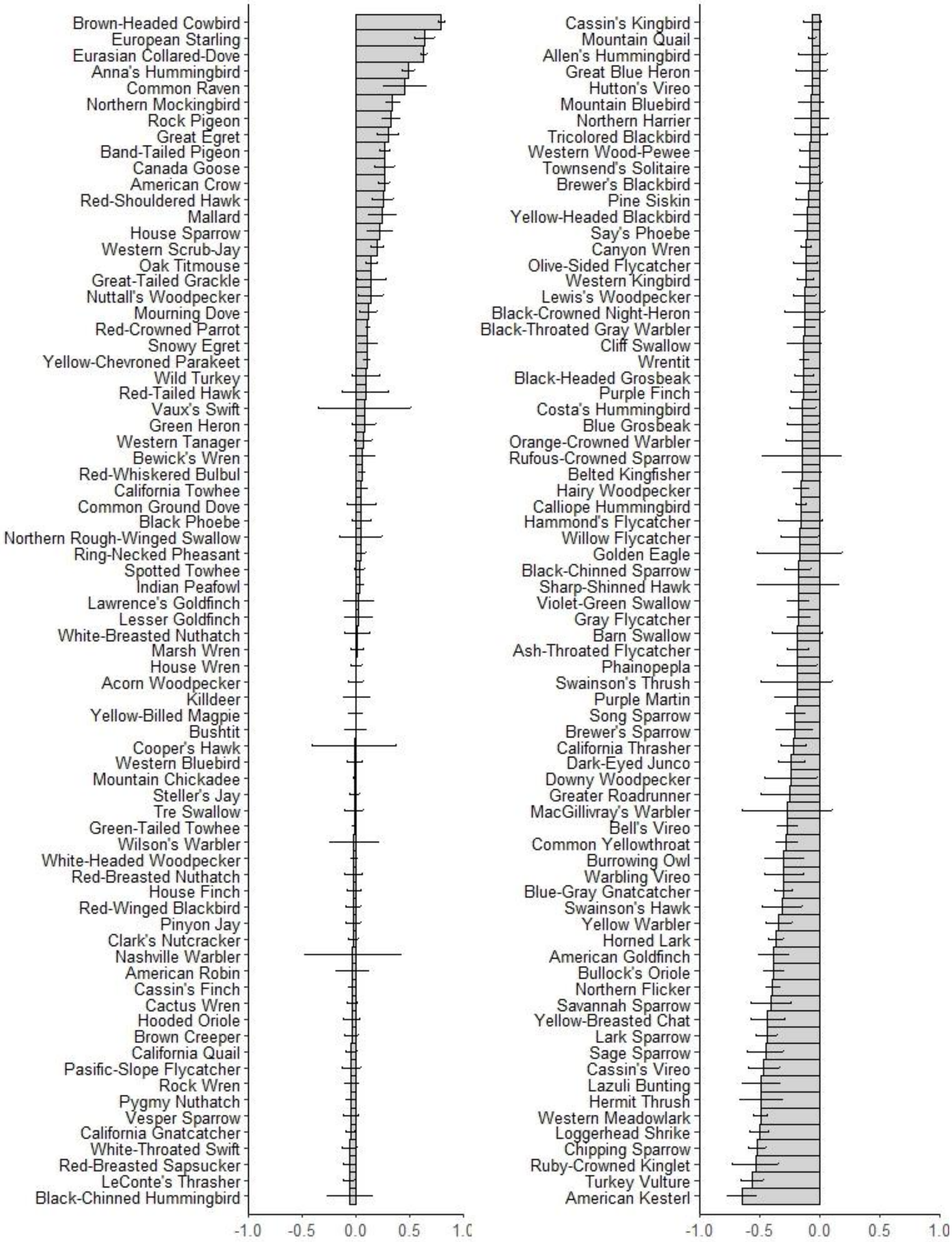

Figure S2: Mean change in probability of occupancy by species. Error bars indicate the 95% credible interval.

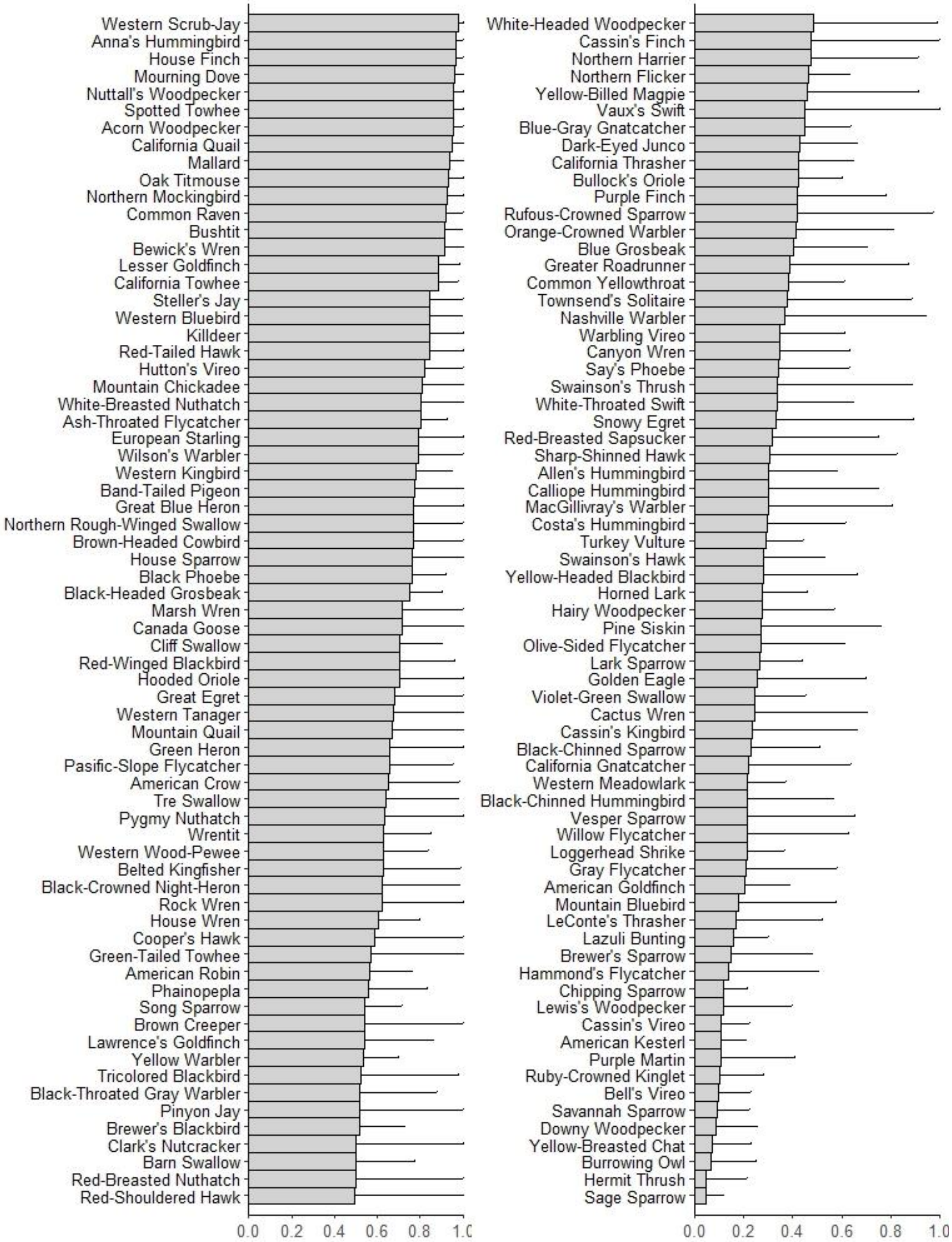

Figure S3: Mean probability of persistence by species. Error bars indicate the 95% credible interval.

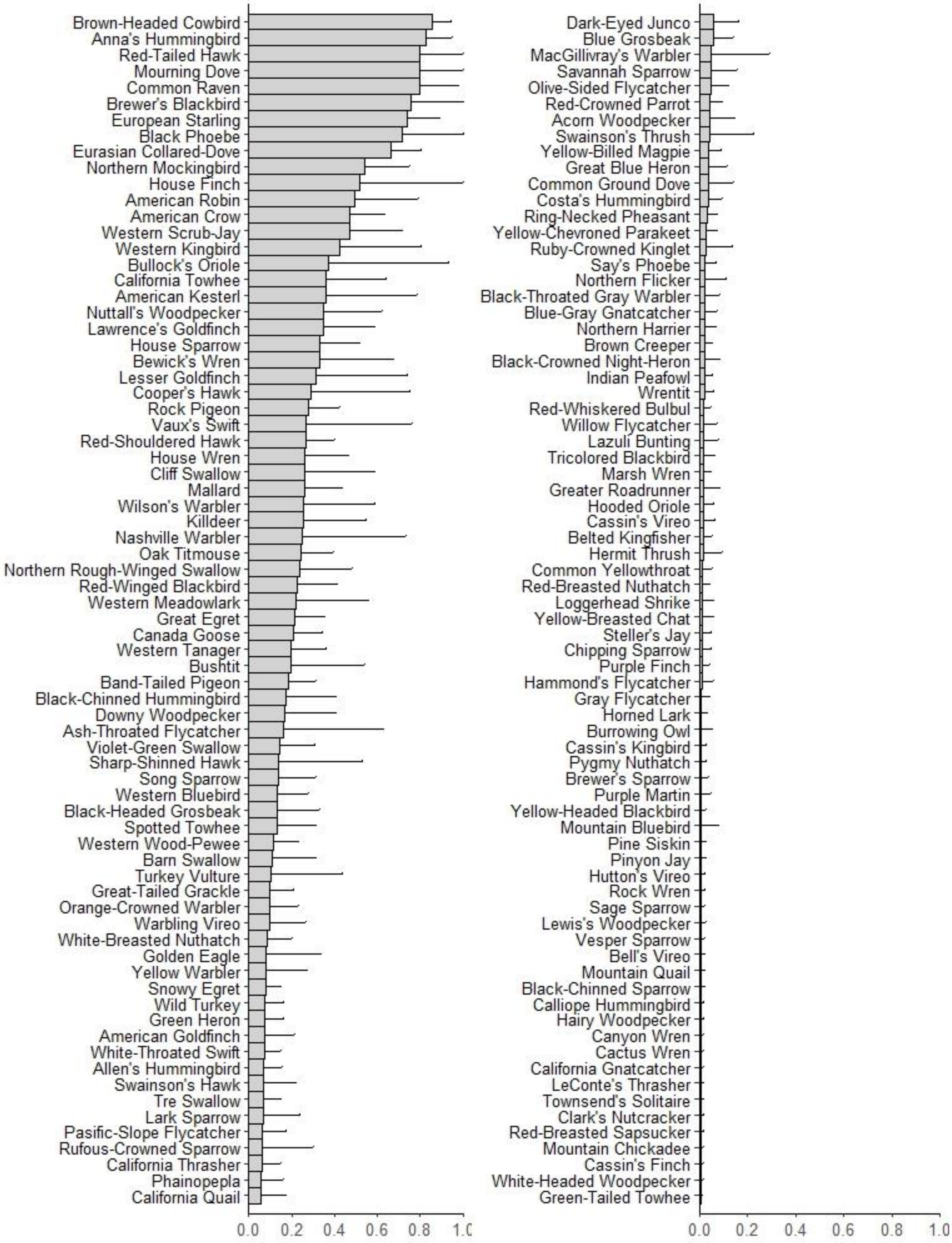

Figure S4: Mean probability of colonization by species. Error bars indicate the 95% credible interval.

Appendix 1: JAGS model code for dynamic multispecies occupancy model

```
model{
  # Community-level (hyper) priors ------------------------------------------------
  tau <- pow(2.25, -2)
  # # Intercepts:
  # Intial occupancy
  occ_int_location ~ dnorm(0, tau)
  occ_int_sigma ~ dt(0, tau, 1) T(0, )
  occ_int_scale <- pow(occ_int_sigma, -2)
  # Detection
  det_int_location ~ dnorm(0, tau)
  det_int_sigma ~ dt(0, tau, 1) T(0, )
  det_int_scale <- pow(det_int_sigma, -2)
  # Survival and colonization
  surv_int_sigma ~ dt(0, tau, 1) T(0, )
  colon_int_sigma ~ dt(0, tau, 1) T(0, )
  for (time in 1:(n_time_periods - 1)) {
    surv_int_location[time] ~ dnorm(0, tau)
    surv_int_scale[time] <- pow(surv_int_sigma, -2)
    colon_int_location[time] ~ dnorm(0, tau)
    colon_int_scale[time] <- pow(colon_int_sigma, -2)
  }
  # # Coefficients:
  # Initial occupancy
  for (cov in 1:n_occ_covs) {
    occ_coef_sigma[cov] ~ dt(0, tau, 1) T(0, )
    occ_coef_location[cov] ~ dnorm(0, tau)
    occ_coef_scale[cov] <- pow(occ_coef_sigma[cov], -2)
```

```
}
# Detection
for (cov in 1:n_det_covs) {
  det_coef_sigma[cov] ~ dt(0, tau, 1) T(0, )
  det_coef_location[cov] ~ dnorm(0, tau)
  det_coef_scale[cov] <- pow(det_coef_sigma[cov], -2)
}
# Survival and colonization
for (cov in 1:n_surv_covs) {
  surv_coef_sigma[cov] ~ dt(0, tau, 1) T(0, )
}
for (cov in 1:n_colon_covs) {
  colon_coef_sigma[cov] ~ dt(0, tau, 1) T(0, )
}
for (time in 1:(n_time_periods - 1)) {
  for (cov in 1:n_surv_covs) {
    surv_coef_location[time, cov] ~ dnorm(0, tau)
    surv_coef_scale[time, cov] <- pow(surv_coef_sigma[cov], -2)
  }
  for (cov in 1:n_colon_covs) {
    colon_coef_location[time, cov] ~ dnorm(0, tau)
    colon_coef_scale[time, cov] <- pow(colon_coef_sigma[cov], -2)
  }
}
# Likelihood loop --------------------------------------------------------
for (species in 1:n_species) {
  # # Species-level intercept and coefficient priors:
  # Occupancy
```

```
occ_int[species] ~ dnorm(occ_int_location, occ_int_scale)
for (cov in 1:n_occ_covs) {
  occ_coef[species, cov] ~ dnorm(occ_coef_location[cov],
                                 occ_coef_scale[cov])
}
# Survival and colonization
for (time in 1:(n_time_periods - 1)) {
  surv_int[species, time] ~ dnorm(surv_int_location[time],
                                  surv_int_scale[time])
  for (cov in 1:n_surv_covs) {
    surv_coef[species, time, cov] ~ dnorm(surv_coef_location[time, cov],
                                          surv_coef_scale[time, cov])
  }
  colon_int[species, time] ~ dnorm(colon_int_location[time],
                                   colon_int_scale[time])
  for (cov in 1:n_colon_covs) {
    colon_coef[species, time, cov] ~ dnorm(colon_coef_location[time, cov],
                                           colon_coef_scale[time, cov])
  }
}
for (site in 1:n_sites) {
  # # Regressions:
  # Initial occupancy state (time = 1)
  logit(occ[species, site, 1]) <- occ_int[species] +
    inprod(occ_coef[species, ], occ_covs[site, ])
  mean_incidence[species, site, 1] <- occ[species, site, 1]
  # Model of changes in occupancy state for time=2, ..., n
  for (time in 1:(n_time_periods - 1)) {
```

```
    logit(surv[species, site, time]) <- surv_int[species, time] +
     inprod(surv_coef[species, time, ], surv_covs[site, time, ])
    logit(colon[species, site, time]) <- colon_int[species, time] +
     inprod(colon_coef[species, time, ], colon_covs[site, time, ])
    mean_incidence[species, site, time + 1] <- surv[species, site, time] *
     incidence[species, site, time] + colon[species, site, time] *
     (1 - incidence[species, site, time])
   }
  }
  # # Detection loops:
  # Species-level intercept and coefficient priors
  det_int[species] ~ dnorm(det_int_location, det_int_scale)
  for (cov in 1:n_det_covs) {
   det_coef[species, cov] ~ dnorm(det_coef_location[cov],
                  det_coef_scale[cov])
  }
  for (site in 1:n_sites) {
   for (time in 1:n_time_periods) {
    for (visit in 1:visits_by_site[site, time]) {
     # Regression
     logit(det[species, visit, site, time]) <- det_int[species] +
      inprod(det_coef[species, 1:(n_det_covs - n_site_det_covs)], det_covs[visit, site, time, ]) +
      inprod(det_coef[species, (n_det_covs - n_site_det_covs+1):n_det_covs],
site_det_covs[site, time, ])
     mean_det_matrix[species, visit, site, time] <-
      det[species, visit, site, time] * incidence[species, site, time]
     # Generate a likelihood for the MCMC sampler by linking the
     # model to the field data
     det_matrix[species, visit, site, time] ~
```

```
          dbern(mean_det_matrix[species, visit, site, time])
        # Simulate the detection matrix that is predicted by the model
        # (used to calculate PPC)
        det_matrix_simulated[species, visit, site, time] ~
          dbern(mean_det_matrix[species, visit, site, time])
      }
      # Partially-latent incidence matrix
      incidence[species, site, time] ~
        dbern(mean_incidence[species, site, time])
    }
  }
 }
}
```

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