

Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds

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Abstract

Predicting biodiversity responses to climate change remains a difficult challenge, especially in climatically complex regions where precipitation is a limiting factor. Though statistical climatic envelope models are frequently used to project future scenarios for species distributions under climate change, these models are rarely tested using empirical data. We used long-term data on bird distributions and abundance covering five states in the western US and in the Canadian province of British Columbia to test the capacity of statistical models to predict temporal changes in bird populations over a 32-year period. Using boosted regression trees, we built presence-absence and abundance models that related the presence and abundance of 132 bird species to spatial variation in climatic conditions. Presence/absence models built using 1970–1974 data forecast the distributions of the majority of species in the later time period, 1998–2002 (mean AUC = 0.79 ± 0.01). Hindcast models performed equivalently (mean AUC = 0.82 ± 0.01). Correlations between observed and predicted abundances were also statistically significant for most species (forecast mean Spearman's $\rho = 0.34 \pm 0.02$, hindcast = 0.39 ± 0.02). The most stringent test is to test predicted changes in geographic patterns through time. Observed changes in abundance patterns were significantly positively correlated with those predicted for 59% of species (mean Spearman's $\rho = 0.28 \pm 0.02$, across all species). Three precipitation variables (for the wettest month, breeding season, and driest month) and minimum temperature of the coldest month were the most important predictors of bird distributions and abundances in this region, and hence of abundance changes through time. Our results suggest that models describing associations between climatic variables and abundance patterns can predict changes through time for some species, and that changes in precipitation and winter temperature appear to have already driven shifts in the geographic patterns of abundance of bird populations in western North America.

Keywords: bird populations, boosted regression trees, climate-envelope models, global change, niche models, Pacific Northwest, species distributions

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Introduction

Understanding the factors driving species geographical distributions is a central issue in ecology (Guisan & Zimmermann, 2000; Gaston, 2003), especially in the context of climate change (Vitousek *et al.*, 1997; Parmesan *et al.*, 2000). Strong empirical evidence has already accumulated that climate warming has caused many species, including birds, to shift their distributions towards higher latitudes and elevations in the temperate zone and on tropical mountains (e.g. Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Wilson *et al.*,

2005; Hitch & Leberg, 2007; Devictor *et al.*, 2008; Chen *et al.*, 2011; Tingley *et al.*, 2012). However, no such consensus has emerged in relation to precipitation changes, partly because far fewer data are available from dry regions and partly because spatial patterns of precipitation change are complex. Accounting for precipitation changes is particularly relevant in the seasonally dry western US, where precipitation is connected to temperature and elevation through orographic precipitation, snowpack, soil moisture storage and latent heat exchange (Cayan, 1996; Heim, 2002; Hamlet *et al.*, 2007). A few analyses of single species (Foden *et al.*, 2007) and ecosystem productivity patterns (Chamaille-Jammes *et al.*, 2006) suggest that moisture-limited systems are also likely to be highly responsive to climatic changes, but multi-species analyses of distribution

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responses are lacking (but see Crimmins *et al.*, 2011; Beale *et al.*, 2013). This is important because the potentially retreating (low latitude/elevation) range boundaries of many temperate zone species may be determined by moisture availability, and moisture availability is a key determinant of ecosystem and species distributions. Here, we evaluate whether distribution and abundance changes of bird species in western North America are linked to changes in climate.

We assess the utility of species-environment models that are parameterised in one time period to predict changes through time (e.g. Johnston *et al.*, 2013). The premise that space and time can be substituted in models underlies the use of distribution models (also known as niche or climate-envelope models) to project possible changes to the geographic ranges of species under climate change. Distribution models test for associations between environmental conditions at a given time and the occurrence or abundance of target species during the same period, to define the bioclimatic conditions where a given species is distributed (Guisan & Zimmermann, 2000). Such envelopes can then be projected forward in time using general circulation models (Araújo & Peterson, 2012) to postulate the locations of future suitable conditions. Species may be threatened by climate change because of disjunctions between current distributions and the location of suitable conditions in future, declines in suitable area, and complete loss of suitable conditions (Peterson *et al.*, 2001; Thomas *et al.*, 2004; Jetz *et al.*, 2007; Stralberg *et al.*, 2009; Lawler *et al.*, 2011). However, the validity of such projections continues to be debated (Botkin *et al.*, 2007; Beale *et al.*, 2008; Araújo & Peterson, 2012).

Critiques of distribution models often invoke lags between climatic conditions and the distributions of species, and confounding factors, such as biotic interactions (e.g. competition, predation), structural habitat associations, or geology, that could strongly mediate potential relationships between the geographical distributions of species and climatic conditions (Hutchinson, 1957). In essence, correlation does not prove causation. This point is well made. However, the key issue in the context of climate change is not whether it is possible to imagine confounding biological and statistical factors that might invalidate projections (it always is), but how well such models actually perform empirically at predicting changes to the abundance patterns and distributions of species through time. Such tests have been reasonably successful over long time periods, for example in using models parameterised using present-day distributions to predict the observed ranges of species at the last glacial maximum, and comparing those projections with the distributions of fossil bones or pollen (Huntley *et al.*, 1993; Ohlemüller *et al.*, 2012; Smith

et al., 2013). Rigorous tests of the capacity of models to predict changes over much shorter periods of time are still needed (but see Araújo *et al.*, 2005; Oliver *et al.*, 2012; Johnston *et al.*, 2013). In part, this knowledge gap arises because of the nature of most presence/absence distributional databases; areas of new colonization or extinction often only represent a relatively small fraction of the total area that a species occupies, and most volunteer-collected distributional data, although extremely valuable, are insufficient to confirm extinctions. Greater statistical power may be available if abundances are also considered, because abundance is a continuous variable, and climate-driven abundance changes may be detected across much larger parts of a species' range. Unfortunately, historical multi-species datasets that include information about changes in abundances over large geographic areas are scarce (see Both *et al.*, 2006; Willis *et al.*, 2008).

Here, we consider how spatial and temporal variation in the climate affects the distributions and geographic abundance patterns of birds. Birds show strong responses to contemporary climate change (Brotons *et al.*, 2007; Devictor *et al.*, 2008), in part because they depend on resources that are closely tied to environmental change (Both *et al.*, 2006; Sillett *et al.*, 2000; Pearce-Higgins *et al.*, 2010). Changes to bird populations provide a useful indicator of the ecological effects of climate change (Jiménez-Valverde *et al.*, 2011), since birds carry out key biotic interactions such as seed dispersal, pollination and top-down control of herbivory (e.g. Bale *et al.*, 2002; Şekercioğlu *et al.*, 2004). We capitalized on a large-scale dataset on the abundance of 132 terrestrial bird species in western North America to test the performance of distribution models in predicting changes in bird distributions and abundances over a 32-year period. Our objectives were to assess the predictive capacity of climate-envelope models over this period, and to establish whether recent precipitation as well as temperature changes have influenced the distribution and abundance changes of birds.

Materials and methods

Study system

Our study system encompasses most of western North America, including California, Nevada, Oregon, Washington and Idaho in the United States, and the Canadian province of British Columbia. Our study area covers a latitudinal range of 32°41'N to 60°00'N (approximately 3000 km south to north) that is sufficiently large to include the entire latitudinal (breeding) distribution of the majority of the species considered (Fig. 1). The longitudinal range is narrower (114°46'W to 138°55'W), but given the region's complex topography ranging from below sea level to 4394 m.a.s.l. and a gradient from

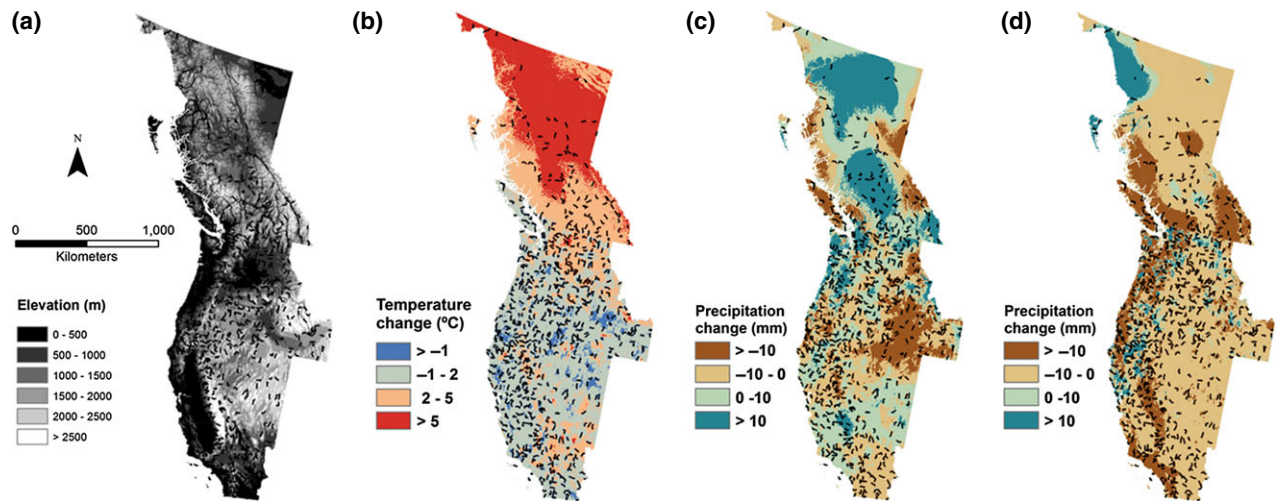


Fig. 1 Panel (a) Map of the study area, showing the topographical heterogeneity of the five US states (California, Idaho, Nevada, Oregon, Washington) and Canadian province of British Columbia included. Panel (b) Change (70–74 to 98–02) in average minimum temperature of the coldest month (January). ΔT_p varies from a cooling of > -1 °C (dark blue) to warming of > 5 °C (dark red). Panel (c) Change in average precipitation of the driest month (July), from a drying of > -10 mm (dark brown) to increased precipitation of > 10 mm (dark blue). Panel (d) Change in average precipitation of the wettest month (December), from a drying of > -10 mm (dark brown) to increased precipitation of > 10 mm (dark blue). BBS routes used in the study are shown in black in all maps.

oceanic to continental climates, it is sufficient to generate conditions ranging from evergreen rainforest to desert. Our study system includes a wide climatic range (Fig. 1), with average monthly temperatures on sampling routes ranging from -29.9 °C (January minimum) to 41.9 °C (July maximum), and monthly total precipitation ranging from 0 (July, driest month) to 629 mm (December, wettest month) depending on location (Table 1).

Bird data

Terrestrial bird species' population data were derived from count data collected as part of the USGS Breeding Bird Survey (BBS, www.pwrc.usgs.gov/bbs, Sauer *et al.*, 2011). These data have been used widely in studies of bird distributions (Robbins *et al.*, 1986, 1989; Peterson, 2003; Phillips *et al.*, 2010). The

BBS survey system consists of 39.4 km linear routes that are located on secondary roads throughout the continental United States and Canada. BBS data has been collected every May or June (breeding season) since 1966 by trained surveyors that recorded every species observed during 3 min counts at 50 point locations spaced at 0.8 km intervals along the route. The survey begins soon after sunrise and surveyors record birds that are seen or heard within 400 m from each point, summing counts over all 50 points in a given year (Bystrack, 1981). BBS data provide an index of population abundance at the scale of an individual route that can be used to estimate trends in relative abundance at various geographic scales. We selected bird species that were present in more than 10% and fewer than 80% of sampling sites in the study system during the selected time periods (to avoid extremely common and extremely rare species), excluding species whose distributions mainly occur

Table 1 List of climate variables included in the analyses. Values are given at route level in each period as they were included in the analyses. Average values are shown for all study sites in the selected period and values in brackets show the ranges of the given variable in the study system

Climate variable	Units	Mean (min–max)	
		1970–1974	1998–2002
June Maximum Temperature	°C	24.7 (13.0 – 39.9)	22.7 (11.0 – 39.1)
June Minimum Temperature	°C	8.8 (0.9 – 23.4)	7.5 (0.1 – 21.7)
June total Precipitation	mm	24.2 (0 – 104.2)	33.6 (0 – 116.9)
July Maximum Temperature	°C	28.5 (16.1 – 41.9)	27.2 (14.3 – 41.0)
July total Precipitation	mm	15.4 (0 – 100.7)	17.9 (0 – 98.9)
January Minimum Temperature	°C	-4.6 (-29.9 – 6.6)	-4.0 (-18.0 – 9.6)
December total Precipitation	mm	125.7 (1.9 – 538.9)	120.4 (0.3 – 629.2)

outside the study region and those for which the region may not contain environmental limits respectively. Aquatic and coastal bird species were also excluded because we did not expect the terrestrial-based BBS routes to sample breeding populations of these species effectively. In total, 132 species satisfied the criteria for analyses.

We considered two 5-year windows, representing an early (1970–1974) and a later period (1998–2002). Five-year periods were considered to reduce sampling variation in abundance caused by observer and interannual weather effects. We used BBS data from 1970, the earliest year when enough routes were available for analysis. The later period was defined by the availability of high-resolution climate data that matched route locations. A given species was considered to be ‘present’ on a particular transect route if it was recorded there in one or more of the 5 years. To avoid possible ‘false zeroes’ in species counts, we only included routes that were sampled in all years during each period (1970–1974 and 1998–2002). Abundance was the average number counted on a route over the 5 year period. This approach has been adopted in previous studies on species distributions that use BBS data (Hitch & Leberg, 2007; Phillips *et al.*, 2010). Finally, we also excluded from analyses those routes that were so close to the ocean that their centroids were located in the water, which would bias estimates of terrestrial climate. This initial screening resulted in a dataset of 642 routes, of which 332 and 541 routes were sampled in the early and later time periods respectively, with 231 sampled in both periods (Fig. 1).

Environmental data

We obtained historical climate data generated by the Parameter Regression of Independent Slope Model (PRISM) (Oregon Climate Service, Corvallis, OR, USA) for the continental United States (Daly *et al.*, 2002). Equivalent data for Canada were provided by the Canadian Forest Service, Natural Resources Canada (<http://cfs.nrcan.gc.ca>). Both climate datasets were created using point meteorological station data, digital elevation models, and other spatial data sets to generate interpolated gridded estimates of monthly, yearly and event-based climatic parameters, such as precipitation, temperature and dew point. We used maps at a spatial resolution of 2.5 arcmin (approximately 3 km cell size at this latitude), as generated by PRISM (Daly *et al.*, 2000). For the 30 arcsec resolution British Columbia data, we resampled to 2.5 arcmin to match the resolution of the PRISM data: i.e. we took the arithmetic means of the 25 constituent 30 arcsec resolution cells to generate each 2.5 arcmin cell value for British Columbia.

We selected a set of seven climatic variables previously reported to be associated with bird species distributions, reflecting conditions in the breeding season and during summer and winter months when the most extreme conditions are likely to be experienced (Green *et al.*, 2008; Jiménez-Valverde *et al.*, 2011). The seven climatic predictors included in the models were: average daily maximum temperature of the hottest month in the study system (July), average daily minimum temperature of coldest month (January) and total precipitation of wettest (December) and driest month (July). We expect July

conditions will affect the nature of the vegetation and food availability, particularly for fledglings (Rivers *et al.*, 2012). Winter (December/January) conditions will affect the nature of the vegetation, the survival of overwintering individuals (Doherty & Grubb, 2002), and also affect the survival of interacting species (that may alter subsequent success in the breeding season) (Robb *et al.*, 2008). The peak breeding period for most birds in the study region was in June, so we also considered maximum temperature, minimum temperature and precipitation for this month. We excluded one of any pair of predictor variables with $R^2 > 0.5$. The only exception was that we did include both maximum temperature in June and July in the same models, partly because BRT models are relatively resilient to overfitting (and should not improve testing with fully independent data), but more importantly because high temperatures could have important and separate impacts on pre- (mostly June) and postfledging (mostly July) survival. The full set of predictor variables included in the analyses is listed in Table 1.

We took the average for each climate variable across the 5 years in each time period, and across all pixels within 1 km of BBS routes, the maximum distance within which birds are likely to be detected in a survey (Betts *et al.*, 2007). Distribution models could fail if there is a mismatch between the spatial resolution of population processes and of the environmental predictor variables (Araújo & Peterson, 2012). It has frequently been noted that the spatial scale of studies strongly affects relative importance of environmental factors associated with species distributions (Johnson *et al.*, 2004; Olivier & Wotherspoon, 2005; Jiménez-Valverde *et al.*, 2011). In this particular case, missing the appropriate spatial scale of the study species may lead to incorrect interpretation of the results (Beale *et al.*, 2008). We therefore repeated analyses using climatic conditions within 20 and 50 km of each route, to represent the subregional or regional scales that have previously been related to bird populations (Tittler *et al.*, 2006). However, model performance was highly correlated across the three spatial scales ($R^2 > 0.8$ in all cases) so we report only the 1 km buffer model performance here.

Changes in both temperature and precipitation showed a spatially patchy pattern between 1970–1974 and 1998–2002 (Fig. 1, Table 1). The north and southern mountain ranges tended to become warmer, whereas remaining areas of the south either stayed about the same or cooled slightly. In summer, some areas became drier and others wetter, whereas most regions became drier in winter (Fig. 1). This spatial heterogeneity in temperature and precipitation changes provides useful variation to assess occupancy and population changes in response to variation in the climate.

Statistical analyses

Model development. Models were developed using the ‘gbm’ package in R (R Development Core Team, 2010) for Boosted Regression Trees analyses, which have been widely used for climatic envelope models (Randin *et al.*, 2009; Carvalho *et al.*, 2010; Engler *et al.*, 2011; Verburg *et al.*, 2011). Boosted Regression Trees (BRTs) are a type of machine-learning method that

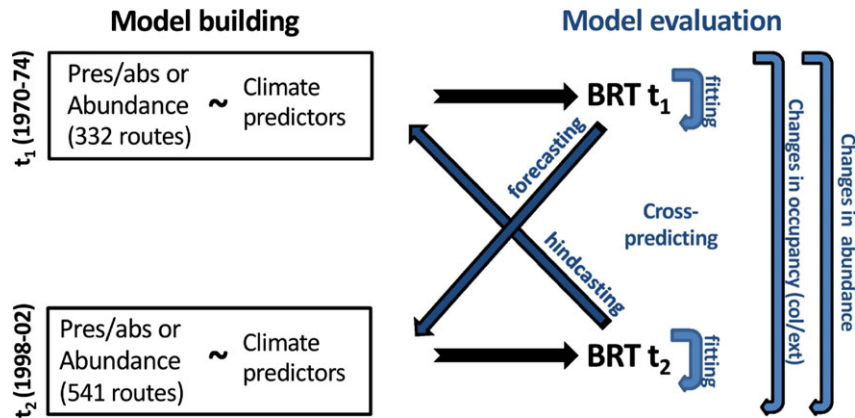


Fig. 2 Flowchart summarizing the model building and evaluation process.

combines the strength of regression trees and boosting; that aims to fit a single parsimonious model. GBMs combine many simple models to give improved predictive performance and provide the capacity to include different types of predictor variables and to accommodate missing data. BRTs exhibit high prediction performance while minimizing the risks of overfitting (Elith *et al.*, 2006). In addition, they are sufficiently flexible to include nonlinear relationships and interactions between predictors (Elith *et al.*, 2008). We generate BRT models with the set of seven climatic variables as predictors and observed occurrence or abundance for each time period as response variables (Fig. 2). Both abundance and occurrence models such as ours are well known to suffer from potential biases caused by imperfect detection (MacKenzie *et al.*, 2003; Kery, 2011). However, we elected not to account for detection in our modelling strategy for four reasons. First, BBS data are not collected using the repeated temporal sample structure required for occupancy modelling (MacKenzie *et al.*, 2003). Second, to date, no machine-learning methods (e.g. BRT) exist that account for imperfect detection. Machine-learning methods such as BRT enable the fitting of complex structures (nonlinearities, interactions) that would be extremely computationally challenging in an occupancy framework. Thirdly, 'occupancy', after accounting for imperfect detection, is a latent variable and therefore impossible to validate on independent data because the 'true' state of independent data are unknown (Welsh *et al.*, 2013). Finally, as our primary objective was SDM validation, and the same search effort was applied to every transect in both time periods, this approach was therefore inappropriate.

Model evaluation. We evaluated both abundance and distribution models in two ways: (i) description of the fit of the original models within a given time period (verification) and (ii) model forecasting and hindcasting with independent data, in our case using models developed during one time period to predict observed patterns in the other period (cross-validation; Araújo & Guisan, 2006; Dobrowski *et al.*, 2011). Given the data (continuous vs. binary) and observed patterns (lack of normality in abundance data), the procedures for verification and cross-validation depended on the distribution of response

variables. We verified the models using data from the same time period used for model development. We calculated the performance of the presence/absence models using AUC (area under the receiving operating characteristic curve) (Fielding & Bell, 1997; Manel *et al.*, 2001; McPherson *et al.*, 2004). Values normally range from 0.5 (no better than random association) to 1 (perfect fit). There is no universally accepted ideal measure of model performance (see Lobo *et al.*, 2008), but AUC has been widely used as a threshold independent metric of model fit and its properties are well understood (Thuiller, 2003; Araújo *et al.*, 2005; Brotons *et al.*, 2007; Pearman *et al.*, 2008; Gutiérrez Illán *et al.*, 2010) (Figure S2). We evaluated abundance models using Spearman's rank correlation coefficients (Spearman's ρ) between predicted (from model-averaged coefficients) against observed abundance values (Fig. 2). We used rank correlations coefficients (ρ) between predicted and observed abundance values because observed count numbers were low for almost all species on some routes (leading to deviations from normality), and for consistency with the analysis of abundance changes between periods (some species showed nonlinear relationships between predicted and observed abundance changes, e.g. Fig. 5). We also tested for correlations between observed and predicted abundance using Pearson's r , but results were not substantively different, so here we report only Spearman ρ , which is a more conservative test.

For cross-validation, we used the models developed in one time period and then used climate data in the other period to predict occurrences or abundance of the selected species in the target routes (Fig. 2). These were compared with the observed measures of occurrence and abundance in the alternative test period. As an additional, more challenging test of the efficacy of climate-envelope models, we used our models to make forecast and hindcast predictions about occurrence and abundance at routes that were not sampled in the alternative time period. We ran the models based on the whole set of routes in each period (332 in 1970–1974 and 541 in 1998–2002) and evaluated their predictive power with the set of routes that were not sampled in the alternate period (101 in 1970–1974 and 309 in 1998–2002). These tests were thus carried out on both spatially and temporally independent data (Bahn & McGill, 2013).

Predicting species distributions and abundances over time. The strongest test of whether the climate variables in (spatial) models are causally linked to species' distributions and abundances is to make predictions about changes over time, and then to test these against observed changes. First, we carried out these analyses using changes in occupancy through time. A given species at a sampling location can (i) colonize, (ii) go locally extinct, (iii) persist or (iv) remain absent during a given period of time (Nichols *et al.*, 1998; MacKenzie *et al.*, 2003). Thus, we identified the routes where each of these states had been observed (changes in occupancy: absence to presence of n individuals, and *vice versa*). We only considered the subset of routes monitored in both time periods to ensure data consistency. The total number of routes that were sampled in both years and therefore included in the analyses was 231 (out of 332 in 1970–1974 and 541 in 1998–2002). Of the 132 target species in our study system, we selected for analysis the species for which local extinction or colonization had occurred for >5 routes over the study period.

To estimate expected change in occupancy, we ran BRTs using data from the first time period to estimate initial occupancy probability ($\hat{\psi}_{11}$). We then predicted to the second period using this first model given changes in climate that occurred on each route ($\hat{\psi}_{12}$). The difference between these values ($\hat{\psi}_{12} - \hat{\psi}_{11}$) was considered the expected change in probability of occupancy ($\Delta\psi$). Prediction accuracy was assessed by comparing $\Delta\psi$ with observed change in occupancy status (Fig. 4). We used a paired *t*-test (98 species) to investigate whether observed change in occupancy (a dichotomous response variable; locally extinct vs. locally colonized sites) was significantly associated with the predicted change in occupancy (a continuous variable).

In the case of the abundance models, which incorporate both abundance changes (on routes populated in both periods) and changes in occupancy (absence to presence of n individuals, and *vice versa*) we followed a similar procedure. To calculate abundance changes, we used the 1970–1974 model to describe initial abundances in the first time period ($\hat{\eta}_{11}$) for each route. We projected abundance in the second time period ($\hat{\eta}_{12}$) using the t1 model parameterized with t2 climate data. The difference ($\Delta\eta$) represents the expected change in abundance on each route ($\hat{\eta}_{12} - \hat{\eta}_{11}$). We then tested the correlation between $\Delta\eta$ and observed abundance changes. Transect routes where a species was absent in both time periods were excluded to avoid the possibility that statistical fits might be exaggerated (large numbers of points with near-zero predicted change and zero change observed). Again, we only considered the subset of routes monitored in both time periods. A total of 132 species satisfied criteria for analysis of abundance changes. We assessed predictive power by calculating Spearman rank correlations (ρ), given that the relationships between predicted and observed abundance changes were not always linear (Fig. 5), with no single transformation proving suitable for all species. For brevity, we report only forecast results for both occupancy and abundance change models. Backcast prediction accuracies were slightly higher and qualitatively similar. A summary of the complete model building/cross-validation process is shown in Fig. 2.

Relative contribution of climate variables. We calculated the relative influence of each predictor in BRTs using the *gbm* package; this provides a measure of the strength of each variable's influence on the total response and is reflected as a proportion (Elith *et al.*, 2008). We recorded the top-ranked explanatory variable for each species, as well as the three top-ranked variables. For each variable, we counted the number of species for which its independent contribution was ranked first, or within the top three (Radford & Bennett, 2007), thus providing an overall estimate of the importance of each variable to bird distributions and abundances in the region. As a further test, we also calculated the relative contribution of the variables for the species with the best-performing models (34 species with Spearman's ρ above 0.4).

Spatial autocorrelation. One of the most common criticisms of the species distribution models is spatial autocorrelation of results, which could lead to spurious relationships and thus, to infer wrong conclusions (Beale *et al.*, 2008). Spatial autocorrelation can influence the reliability of biogeographical analyses, particularly based on sample sites separated by short geographic distances (Algar *et al.*, 2009). We tested for spatial autocorrelation in residuals of both presence-absence and abundance models using correlograms (Moran's *I*; Fortin *et al.*, 1989; Betts *et al.*, 2006).

Results

Model verification

Distribution models generally performed well for most species within both time periods (internal validation). For presence/absence models, 87% (1970–1974) and 80% of species (1998–2002) showed AUC values >0.8, with mean (\pm SE) AUCs of 0.88 ± 0.01 and 0.87 ± 0.01 for the two periods respectively (Fig. 3) (Figure S2). Correlations between observed and predicted abundance were also quite high when tested within time periods; Average ρ (\pm SE) was 0.47 ± 0.02 for 1970–1974 (94% of species showing significant associations; $P < 0.01$) and 0.49 ± 0.01 for 1998–2002 (98% of species showing significant associations; $P < 0.01$; Fig. 3).

Model cross-validation between time periods

Prediction success was lower in validation than in verification, though not substantially. When forecasting using presence/absence models, mean (\pm SE) AUC was 0.77 ± 0.01 . When hindcasting, mean (\pm SE) AUC value was 0.81 ± 0.02 for presence/absence models (Fig. 3). In total, 40% (forecasting) and 59% (hindcasting) of the species showed excellent (AUC > 0.8) predictive performance between time periods. In abundance models, forecast results were positively correlated with observed abundance in the second time period [mean

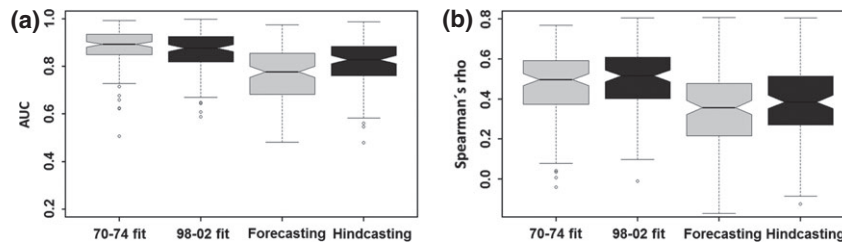


Fig. 3 Summary of model performance evaluation for (a) distribution (presence/absence) and (b) abundance models. Presence/absence models were evaluated via AUC and abundance models were evaluated using Spearman's rank correlation coefficients between observed and predicted abundance of each target species at each route.

$\rho = 0.34 \pm 0.02$ (90% out of 132 species significant at $P < 0.01$). Hindcast results yielded slightly higher correlations between observed and predicted abundances [$\rho = 0.38 \pm 0.02$ (92% out of 132 species significant with $P < 0.01$)] (Fig. 3). Abundance models for 61% and 72% of species (for forecasting and hindcasting respectively) showed correlations $\rho > 0.3$. For each analysis, the improved performance of hindcast predictions is likely to reflect the higher number of routes available for model building in the later period.

Performance of the abundance models (Spearman ρ) were significantly correlated with those of the presence/absence models (AUC) in both periods (Spearman $\rho = 0.59$ (1970–1974 models); Spearman $\rho = 0.68$ (1998–2002 models). $N = 132$ in both cases), suggesting common drivers of abundance and distributions. Results obtained in verification and cross-validation for the full set of target species are shown in Table S1. To test the sensitivity of our results to the statistical model, we also applied stepwise logistic regressions to generate climate-envelope models for both presence/absence and abundance. These gave very similar results in making predictions between time periods, but the AUC when using Boosted Regression Trees was higher for 95% of species (Figure S1).

Testing changes in bird occupancy and abundance through time

We tested the capacity of models to predict occupancy changes through time for 98 species that satisfied criteria for analyses (Fig. 4). Mean change in predicted suitability of colonized routes was significantly higher, i.e. more positive, than for routes that went locally extinct (paired t -test, $t = 3.094$; $P < 0.005$; $N = 98$). However, results varied widely across species (Fig. 4). In general, models predicted local extinctions better than the local colonizations. Average climate suitability decreased over time in the routes for seventy of the 98 species which went locally extinct. Average climate suitability increased in colonized routes for 52 species (Fig. 4).

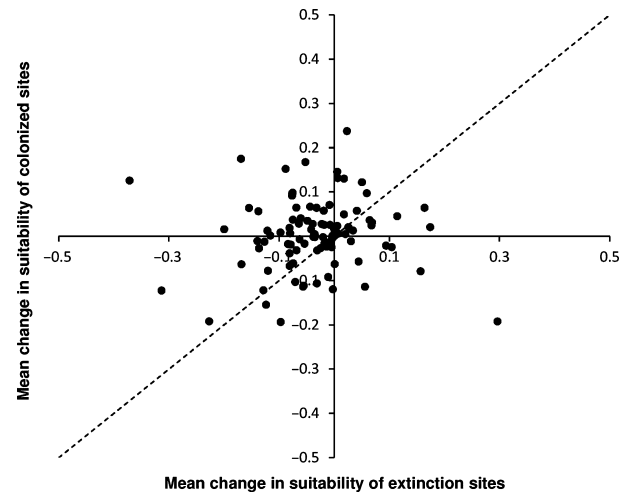


Fig. 4 Plot of mean change in suitability of colonized vs. extinct routes for the target species (each species is represented by a black dot). The dashed line shows no explanation ability (same change in suitability for colonized and extinct routes). Local colonization/extinction of the species located above the line (ideally in the top-left quadrant of the plot) are predicted by the occupancy models through time.

In predicting changes in abundance over time, 71 out of 132 species showed significant correlations between observed and predicted changes (mean $\rho = 0.28 \pm 0.02$, across all species). Again, model quality varied widely, with 61 species (46%) showing weak predictive power ($\rho < 0.2$), 24 species (18%) showing some level of predictive power ($0.2 > \rho < 0.5$) and 47 species (36%) showing correlations > 0.5 (Fig. 5). Model performance for one high-performance and one medium-performance example species are shown in Fig. 5. The purple finch (*Haemorrhous purpureus*) represents a species with a typical northern distribution in North America, whereas loggerhead shrike (*Lanius ludovicianus*) has a typical southern distribution. For both species, there is some indication that climate-related declines are better predicted than increases (Fig. 5). This is consistent with the results obtained in the occupancy change models

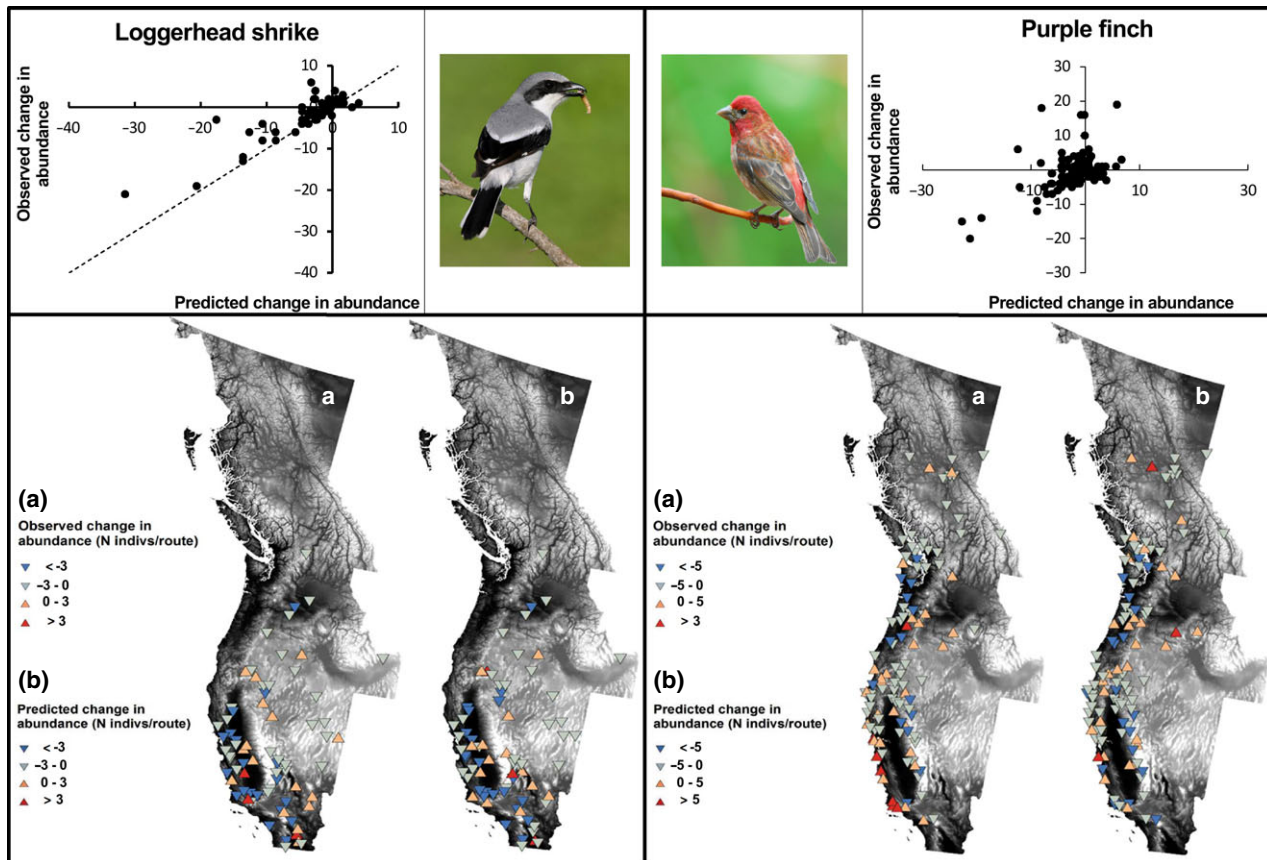


Fig. 5 Plots of observed and predicted abundance changes for two exemplar species, Loggerhead shrike (*Lanius ludovicianus*) (Left), and Purple finch (*Haemorhous purpureus*) (Right). Scatter plots show evaluation of the abundance models through time (Loggerhead shrike, Spearman's ρ of 0.64, based on 72 routes; Purple finch, Spearman's ρ of 0.33, based on 110 routes). Maps show locations of observed (a panels) and predicted (b panels) abundance changes.

where models tended to better predict extinctions than colonizations.

The residuals of abundance models were not spatially autocorrelated for the majority of the species. Ninety-five species showed no significant ($P > 0.05$) autocorrelation at any distance classes. Furthermore, only 12 out of 132 species showed Moran's $I > 0.2$ at any spatial lag, which is generally considered to reflect strong spatial autocorrelation (see full results in Table S2, detailed plots for exemplar species in Figure S3) (Lichstein *et al.*, 2002).

Relative contribution of climate variables

Overall, precipitation was a more important predictor than temperature in both distribution and abundance models (Fig. 6). This conclusion held whether we considered the single top variable in each species' model, or whether a variable was one of the three top predictors (Fig. 6). Figure 6 (lower panel) shows very similar results obtained when considering only the 34 species

with evaluation coefficients (Spearman's ρ) above 0.4. Precipitation in the wettest month (December) was particularly important, with additional contributions from June and July precipitation (Fig. 6). January temperature was, on average, the most important temperature variable included in our models. Hence, the abundance changes that could be predicted by the models were mainly driven by spatio-temporal changes in precipitation and warming trends in winter temperature over time.

Discussion

Our results show that climate-envelope models had considerable capacity for describing the abundance and distribution of bird species in western North America. This is consistent with previous studies showing high predictive ability for distribution models that are trained and tested in the same time period (Renwick *et al.*, 2012; la Sorte & Jetz, 2012; Foden *et al.*, 2013; Smith *et al.*, 2013). Further, our models generally

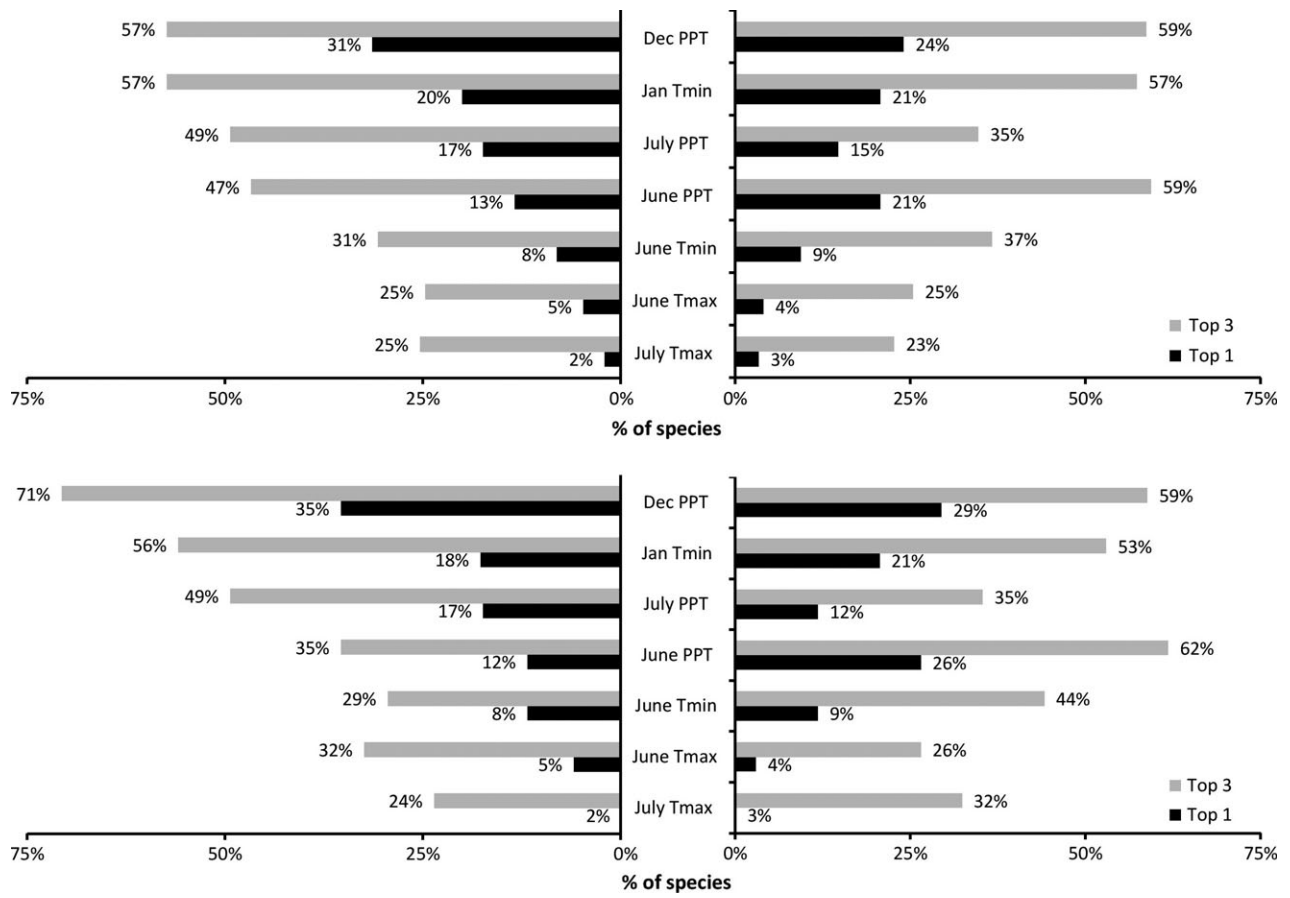


Fig. 6 (Upper panel) Relative contribution of the climate factors included in the models. Plot shows results obtained in presence/absence models (left panel) and abundance models (right panel). Black bars show the percentages (x axes) of models where a given climate variable was ranked as the most important according to its relative contribution. Grey bars show the percentages of models where a given variable was ranked as one of the top three most important variables. Results are shown for the forecasting evaluation only. Lower panel shows the same results, but only for the target species that obtained an evaluation performance (Spearman's ρ) above 0.4 (34 species).

performed well at predicting both occupancy and abundance in alternative time periods (transferability). This is perhaps not surprising given the relatively short time period over which our models predicted (32 years); one would expect there to be temporal autocorrelation in bird distributions, explained partly by an inertia in the distribution of the plant species and climatic envelopes on which they depend (Araújo *et al.*, 2005; Botkin *et al.*, 2007; Rapacciuolo *et al.*, 2013; Watling *et al.*, 2013).

More telling was our finding that, for some species, climate-envelope models were also capable of predicting abundance and occupancy changes across the western portion of the continent; 54% of the species we examined showed significant correlations between predicted and observed abundance changes. Though these models are still correlative, they substantially reduce two problems in climate-envelope model validation: (i)

they are free from problems of temporal autocorrelation in model predictions that would lead to high quality models based solely on the tendency of species to remain at certain population levels or distributions over short time periods (Araújo *et al.*, 2005; Rapacciuolo *et al.*, 2013); (ii) they are less likely than static models to be confounded with biotic variables that show similar distributions to climate; for example, birds are known to be strongly associated with vegetation structure and composition (MacArthur & MacArthur, 1961). Our finding that changes in bird abundance and occupancy are predicted by climate provides stronger evidence that climate itself is an important driver of bird populations – even over relatively short temporal scales. This role may be direct (via thermal limitations; *sensu* Jankowski *et al.*, 2013) or indirect – propagated through influences to, for example, the phenology of vegetation and/or food availability (Both *et al.*, 2006).

Model prediction success is expected to decline as one moves from verification (testing against the data used to build the model), to cross-validation (testing against observed patterns in another time period) and temporal prediction (changes in abundance patterns in space and time) (Araújo *et al.*, 2005). Our models support this expectation; abundance models trained and tested in 1970–1974 (i.e. verification) showed high concordance with observed data ($\rho = 0.47$). In cross-validation to a new time period, correlations dropped ($\rho = 0.34$) and then declined further when predicting geographical patterns of abundance changes across time periods ($\rho = 0.28$). Nonetheless, predictions of temporal changes in abundance patterns were strong ($\rho > 0.5$) for over a third of the species.

Though still scarce, a number of recent studies have tested for the transferability of climate-envelope models in space and time for mammals (Rubidge *et al.*, 2012), plants (Pearman *et al.*, 2008), insects (Kharouba *et al.*, 2009) and birds (Johnston *et al.*, 2013; Rapacciuolo *et al.*, 2013). Superficially, the degree of climate-envelope model success appears to vary widely across studies and taxa, but much of this variability is accounted for by whether or not studies attempted to model occupancy change, or simply model transferability. Generally, studies that built models in time t_1 and predict distributions in t_2 report optimistic results (Dobrowski *et al.*, 2011; Watling *et al.*, 2013). In contrast, Rapacciuolo *et al.* (2013) recently found that although climate-envelope models for plants, birds and butterflies did well at predicting distributions (transferability was high), performance was poor when they attempted to predict changes in occupancy status at range edges. Our findings support this result for a substantial number of species (61/132, 48% of models showed correlations < 0.2). These results provide an important cautionary note: for some species, high explanatory power on temporally independent records does not necessarily indicate a model's ability to predict changes through time. However, the rest of the species we considered showed significant, and in some cases strong, correlations between observed and predicted abundance changes.

One possible explanation for the higher agreement between predicted and observed abundance changes in our study compared to Rapacciuolo *et al.* (2013) lies in the order of magnitude greater geographical scale of our study (2 308 000 km² vs. 229 848 km²). This permitted us to encompass the full latitudinal extent of many species' ranges. Several studies have shown that it is particularly important to include the complete species' environmental range to achieve more accurate predictions (Pearson *et al.*, 2002; Thuiller *et al.*, 2004; Barbet-Massin *et al.*, 2010) and that missing the climatic limits

of the species is more likely lead to the conclusion that distributions of species are not determined by climate (Beale *et al.*, 2008). Our study is one of the first to demonstrate that climate-envelope models predict species distributions and abundances in new, independent locations (see Rubidge *et al.*, 2012).

Though the majority of our models predicting occupancy and abundance changes were significantly correlated with observed changes, for most species substantial variation remained unexplained. It is well known that a wide range of nonclimatic factors drive biodiversity responses – many of which remain challenging to incorporate into SDMs. First, land-use change has clear potential to limit the efficiency with which even fairly vagile species can 'keep pace' with climate change (Jetz *et al.*, 2007). Highly fragmented habitat distributions may preclude dispersal to patches that have newly emerged as part of a species' fundamental niche (Opdam & Wascher, 2004). Few efforts to date have quantitatively examined the degree to which land-use change interacts with climate to drive distributions (Luoto *et al.*, 2007). Second, biotic relationships (e.g. competition, predation, mutualism) all play a role in driving distributions (Blois *et al.*, 2013). Though new techniques are emerging to explicitly incorporate such biotic factors (Heikkinen *et al.*, 2007), these have not been extensively validated to determine the degree to which they improve model predictions over longer time periods (but see Rubidge *et al.*, 2012). Third, the spatial resolution of most climatic envelope models tends to be in the order of 1–100 km² – a scale which is likely mismatched with the scale of perception by many organisms (Gillingham *et al.*, 2012), including birds. A number of studies have recently acknowledged that fine-scale variability in thermal and precipitation regimes have the potential to provide 'refugia' or 'buffering' against landscape or regional trends in climate (Dobrowski, 2011; Moritz & Agudo, 2013). Unfortunately, long-term data on animal distributions, including the data used in this study, are rarely collected at sufficiently fine spatial resolutions to allow for modelling (let alone validating) such microclimatic effects. Nevertheless, it is important to note that despite these additional sources of variation, climate variables alone successfully predicted both abundance and distributional changes for many of the species we examined. We expect that new efforts to incorporate physiological tolerances (Jankowski *et al.*, 2013), dispersal behaviour (la Sorte & Jetz, 2010), and fine-scale land cover data (Shirley *et al.*, 2013) will improve upon the models we report here.

An additional source of variation may arise from the nature of the count data analysed. Though quantifying abundance using 5-year 'windows' undoubtedly

increased detections, and hence noise relating to detectability, the lack of within-year repeat counts in BBS data precludes accounting statistically for biases relating to imperfect detection (MacKenzie *et al.*, 2003). Nevertheless, it is highly unlikely that imperfect detection biased our results *in favour* of SDMs that validate well on independent data.

Most studies of how climate change alters the distributions of species have emphasized the effects of temperature (Walther *et al.*, 2002; Thomas *et al.*, 2004; Chen *et al.*, 2011), but it has been argued that precipitation could exert an equally important role for some organisms (Tingley *et al.*, 2012; Beale *et al.*, 2013). Precipitation can affect bird populations directly, for example through nestling survival (Sillert *et al.*, 2000; Anctil *et al.*, 2014), and indirectly by altering the abundance or availability of invertebrate prey (Carroll *et al.*, 2011), the flowering and fruiting of plant species, the abundance and distribution of disease vectors, and more generally through its impacts on vegetation structure (Mac Nally *et al.*, 2014). With the exception of minimum January temperature, the three precipitation variables featured more strongly in models than did the remaining temperature variables for most species (Fig. 6). Our study thus confirms the importance of considering precipitation in future projections of species under climate change. We hypothesize that precipitation is an important determinant of range retreats in northern species that experience increased desiccation of their habitats in the south, and may facilitate the expansion of drought-tolerant species from the south. However, precipitation change is complex in mountainous terrain (Fig. 1), which has resulted in complex patterns of predicted and observed geographic patterns of abundance change (Fig. 5). Hence, different species may be shifting their distributions in quite variable directions; a single species even may show variation in the direction of shifts in different regions, depending on which environmental variables are limiting and the degree to which they are changing (Root & Schneider, 1993; Root *et al.*, 2003).

Interestingly, winter conditions (precipitation in the wettest month, December, and temperature in the coldest month, January) were the most important predictor variables for most species. For resident species, this may reflect overwinter physiological stress and food availability which in turn affects survival (Doherty & Grubb, 2002; Robinson *et al.*, 2007), but for migrants that are absent during these periods, such changes likely reflect lagged climate effects. For instance, warmer winter temperatures would affect rates of snow-melt, which in turn influences moisture availability and therefore ecosystem productivity during the summer months. Moreover, moisture storage carry-over also

affects air temperature through latent heat exchanges (Porporato *et al.*, 2004; Nolin & Daly, 2006).

The predictive power of climate-envelope models for birds exhibited variable success across species, but declined as data independence increased. Nevertheless, we provide evidence that climate-envelope models are capable of predicting abundance changes through time for a third to half of species, suggesting that climate is driving the changes. Over the 32-year period considered, precipitation was a major determinant of geographic-scale changes in the abundance patterns of terrestrial bird species in western North America. Our results for birds could therefore be considered a 'best case' scenario with respect to the transferability of climate-envelope models because of their relatively high dispersal abilities, and other taxa might show lower prediction success due to lags in dispersal (Ko *et al.*, 2011). A critical next step will be to evaluate the role of life history traits such as dispersal capacity, fecundity and longevity in predicting climate-envelope model transferability.

In conclusion, our ability to predict geographic patterns of abundance change through time demonstrates the importance of climate, particularly precipitation, to the changing distributions of a third to a half of the species studied, but the variation explained also implies that factors other than climate, such as dispersal, land-use and heterospecifics are also important determinants of large-scale distribution change. The quest for improved model predictions will inevitably involve attempting to minimize trade-offs between the limited spatial extent of fine-resolution data depicting organism's responses to land use/land cover and biotic interactions (which produce detailed, accurate models of local places that are hard and thus problematic to generalize) and the desire to create broad-scale models that are relevant to understanding global change.

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Supporting Information

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

Figure S1. Summary of results obtained in the species distribution model evaluation using the later period (98–02) for an exemplar set of 27 species. Model evaluation is shown as area under the receiver operating characteristic curve values (AUC). AUC values are shown for stepwise Logistic Regression (LR) (in black) and Generalized Boosted Regression Models (gbm) (in grey).

Figure S2. Receiving operating characteristic (ROC) curve obtained in the forecasting using models of two exemplar species: (a) Purple finch (*Haemorhous purpureus*), AUC = 0.83, and (b) Loggerhead shrike (*Lanius ludovicianus*) AUC = 0.89.

Figure S3. Spatial autocorrelation analyses for two of the target species based on Moran's I (Montecarlo test, 500 permutations). The residuals of species were not highly spatially autocorrelated with $I < 0.2$ (panel A). Fitted values vs. observed data (panel B). Map of the distribution of residuals (panels C and D).

Table S1. Summary of the results obtained in the two evaluations (fitting and cross-predicting) of gbm of the target species. AUC (presence/absence models) or Spearman's correlation coefficient (abundance models) is shown in each case, and respective *P*-value of the models (ns = nonsignificant; **P* < 0.05; ***P* < 0.01; ****P* < 0.001). *N* = 332 sites (1970–74); *N* = 541 sites (1998–02).

Table S2. Summary of the results obtained in the Spatial Autocorrelation analysis of the target species. Moran's I and *P*-value of the autocorrelogram is shown for each species (ns = nonsignificant; **P* < 0.05; ***P* < 0.01; ****P* < 0.001).