Open Access Articles

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

Oregon State
UNIVERSITY
OSU

1 **Precipitation and winter temperature predict long-term range-scale**

2 **abundance changes in Western North American birds**

3 **Javier Gutiérrez Illán*†, Chris D. Thomas†, Julia A. Jones‡, Weng-Keen Wong §, Susan**

4 **M. Shirley*, and Matthew G. Betts***

5 ** Department of Forest Ecosystems and Society. Oregon State University, Corvallis, Oregon*

6 *97331 USA*

7 *† Department of Biology (Area 18). University of York, Heslington, York YO10 5DD UK*

8 *‡ Department of Geography, College of Earth, Ocean, and Atmospheric Sciences, Oregon*

9 *State University, Corvallis, Oregon, 97331 USA*

10 **§** *School of Electrical Engineering & Computer Science. Kelley Engineering Center. Oregon*

11 *State University, Corvallis, Oregon, 97331 USA*

12

13 Author for correspondence: Javier Gutiérrez Illán, Department of Biology (Area 18).

14 University of York, Heslington, York YO10 5DD UK

15 Tel: (+44) 74 3532 1468; Fax: (+34) 91 664 7490; E-mail: javier.illan@oregonstate.edu

16 javier.g.illan@gmail.com

17 Running headline: *Effects of climate change on the birds of western North America*

18

1   **Abstract**

2   Predicting biodiversity responses to climate change remains a difficult challenge, especially in

3   climatically complex regions where precipitation is a limiting factor.   Though statistical

4   climatic envelope models are frequently used to project future scenarios for species

5   distributions under climate change, these models are rarely tested using empirical data. We used

6   long-term data on bird distributions and abundance covering five states in the western US and

7   in the Canadian province of British Columbia to test the capacity of statistical models to predict

8   temporal changes in bird populations over a 32-year period. Using boosted regression trees, we

9   built presence-absence and abundance models that related the presence and abundance of 132

10   bird species to spatial variation in climatic conditions.   Presence/absence models built using

11   1970-74 data forecast the distributions of the majority of species in the later time period, 1998-

12   2002 (mean AUC = 0.79 ± 0.01). Hindcast models performed equivalently (mean AUC = 0.82

13   ± 0.01). Correlations between observed and predicted abundances were also statistically

14   significant for most species (forecast mean Spearman´s $\rho = 0.34 \pm 0.02$, hindcast $= 0.39 \pm 0.02$).

15   The most stringent test is to test predicted *changes* in geographic patterns through time.

16   Observed changes in abundance patterns were significantly positively correlated with those

17   predicted for 59% of species (mean Spearman´s $\rho = 0.28 \pm 0.02$, across all species). Three

18   precipitation variables (for the wettest month, breeding season, and driest month) and minimum

19   temperature of the coldest month were the most important predictors of bird distributions and

20   abundances in this region, and hence of abundance changes through time. Our results suggest

21   that models describing associations between climatic variables and abundance patterns can

22   predict changes through time for some species, and that changes in precipitation and winter

23   temperature appear to have already driven shifts in the geographic patterns abundance of bird

24   populations in western North America

1   **Key-words:** bird populations, boosted regression trees, climate envelope models, global

2   change, niche models, species distributions, Pacific Northwest.

3   **Introduction**

4   Understanding the factors driving species geographical distributions is a central issue in ecology

5   (Guisan & Zimmermann, 2000; Gaston, 2003), especially in the context of climate change

6   (Parmesan *et al.*, 2000; Vitousek *et al.*, 1997). Strong empirical evidence has already

7   accumulated that climate warming has caused many species, including birds, to shift their

8   distributions towards higher latitudes and elevations in the temperate zone and on tropical

9   mountains (e.g., Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Wilson *et al.*, 2005; Hitch

10   & Leberg 2007; Chen *et al.*, 2011; Devictor *et al.*, 2008; Tingley *et al.*, 2012). However, no

11   such consensus has emerged in relation to precipitation changes, partly because far fewer data

12   are available from dry regions and partly because spatial patterns of precipitation change are

13   complex. Accounting for precipitation changes is particularly relevant in the seasonally dry

14   western US, where precipitation is connected to temperature and elevation through orographic

15   precipitation, snowpack, soil moisture storage, and latent heat exchange (Cavan, 1996; Heim,

16   2002; Hamlet *et al*, 2007) . A few analyses of single species (Foden *et al.*, 2007) and ecosystem

17   productivity patterns (Chamaille-Jammes *et al.*, 2006) suggest that moisture-limited systems

18   are also likely to be highly responsive to climatic changes, but multi-species analyses of

19   distribution responses are lacking (but see Crimmins *et al.*, 2011; Beale *et al.*, 2013). This is

20   important because the potentially retreating (low latitude/elevation) range boundaries of many

21   temperate zone species may be determined by moisture availability, and moisture availability

22   is a key determinant of ecosystem and species distributions. Here we evaluate whether

23   distribution and abundance changes of bird species in western North America are linked to

24   changes in climate.

1   We assess the utility of species-environment models that are parameterised in one time

2   period to predict changes through time (e.g. Johnston *et al*. 2013). The premise that space and

3   time can be substituted in models underlies the use of distribution models (also known as niche

4   or climate envelope models) to project possible changes to the geographic ranges of species

5   under climate change.   Distribution models test for associations between environmental

6   conditions at a given time and the occurrence or abundance of target species during the same

7   period, in order to define the bioclimatic conditions where a given species is distributed (Guisan

8   & Zimmermann, 2000). Such envelopes can then be projected forward in time using general

9   circulation models (Araújo & Peterson, 2012) to postulate the locations of future suitable

10   conditions.   Species may be threatened by climate change because of disjunctions between

11   current distributions and the location of suitable conditions in future, declines in suitable area,

12   and complete loss of suitable conditions (Peterson *et al*., 2001; Thomas *et al*., 2004; Jetz *et al*.,

13   2007; Stralberg *et al*., 2009; Lawler *et al*., 2011).   However, the validity of such projections

14   continues to be debated (Botkin *et al*., 2007; Beale *et al*., 2008; Araújo & Peterson, 2012).

15   Critiques of distribution models often invoke confounding factors, such as biotic

16   interactions (e.g., competition, predation), structural habitat associations, or geology, that could

17   strongly mediate potential relationships between the geographical distributions of species and

18   climatic conditions (Hutchinson, 1957). In essence, correlation does not prove causation. This

19   point is well made. However, the key issue in the context of climate change is not whether it is

20   possible to imagine confounding biological and statistical factors that might invalidate

21   projections (it always is), but how well such models actually perform empirically at predicting

22   changes to the abundance patterns and distributions of species through time. Such tests have

23   been reasonably successful over long time periods, for example in using models parameterised

24   using present-day distributions to predict the observed ranges of species at the last glacial

25   maximum, and comparing those projections with the distributions of fossil bones or pollen

1   (Huntley *et al*., 1993; Ohlemüller *et al*., 2012; Smith *et al*., 2013). Rigorous tests of the capacity

2   of models to predict changes over much shorter periods of time are still needed (but see Araújo

3   *et al*., 2005; Oliver *et al*., 2012; Johnston *et al*. 2013). In part, this knowledge gap arises because

4   of the nature of most presence/absence distributional databases; areas of new colonisation or

5   extinction often only represent a relatively small fraction of the total area that a species

6   occupies, and most volunteer-collected distributional data, although extremely valuable, are

7   insufficient to confirm extinctions. Greater statistical power may be available if abundances

8   are also considered, because abundance is a continuous variable, and climate-driven abundance

9   changes may be detected across much larger parts of a species' range. Unfortunately, historical

10 multi-species datasets that include information about changes in abundances over large

11 geographic areas are scarce (see Both *et al*., 2006; Willis *et al*., 2008).

12 Here, we consider how spatial and temporal variation in the climate affects the

13 distributions and geographic abundance patterns of birds. Birds show strong responses to

14 contemporary climate change (Brotons *et al*., 2007; Devictor *et al*., 2008), in part because they

15 depend on resources that are closely tied to environmental change (Both *et al*., 2006: Sillett *et*

16 *al*., 2000: Pearce-Higgins *et al*. 2010). Changes to bird populations provide a useful indicator

17 of the ecological effects of climate change (Jiménez-Valverde *et al*., 2011), since birds carry

18 out key biotic interactions such as seed dispersal, pollination and top-down control of herbivory

19 (e.g., Bale *et al*., 2002; Şekercioğlu *et al*., 2004). We capitalized on a large-scale dataset on

20 the abundance of 132 terrestrial bird species in western North America to test the performance

21 of distribution models in predicting changes in bird distributions and abundances over a 32-

22 year period. Our objectives were to assess the predictive capacity of climate envelope models

23 over this period, and to establish whether recent precipitation as well as temperature changes

24 have influenced the distribution and abundance changes of birds.

25 **MATERIALS & METHODS**

1 **Study system**

2 Our study system encompasses most of western North America, including California, Nevada,

3 Oregon, Washington and Idaho in the United States, and the Canadian province of British

4 Columbia. Our study area covers a latitudinal range of 32º41'N to 60º00'N (approximately

5 3000 km south to north) that is sufficiently large to include the entire latitudinal (breeding)

6 distribution of the majority of the species considered (Fig. 1). The longitudinal range is

7 narrower (114º46'W to 138º55'W), but given the region's complex topography ranging from

8 below sea level to 4394 m.a.s.l. and a gradient from oceanic to continental climates, it is

9 sufficient to generate conditions ranging from evergreen rainforest to desert. Our study system

10 includes a wide climatic range (Fig. 1), with average monthly temperatures on sampling routes

11 ranging from -29.9ºC (January minimum) to 41.9ºC (July maximum), and monthly total

12 precipitation ranging from 0 (July, driest month) to 629 mm (December, wettest month)

13 depending on location (Table 1).

14

15 **Bird data**

16 Terrestrial bird species´ population data were derived from count data collected as part of the

17 USGS Breeding Bird Survey (BBS, www.pwrc.usgs.gov/bbs, Sauer *et al*., 2011). These data

18 have been used widely in studies of bird distributions (Robbins *et al*., 1986, 1989; Peterson

19 2003; Phillips *et al*., 2010). The BBS survey system consists of 39.4 km linear routes that are

20 located on secondary roads throughout the continental United States and Canada. BBS data has

21 been collected every May or June (breeding season) since 1966 by trained surveyors that

22 recorded every species observed during 3 minute counts at 50 point locations spaced at 0.8 km

23 intervals along the route. The survey begins soon after sunrise and surveyors record birds that

24 are seen or heard within 400 m from each point, summing counts over all 50 points in a given

1   year (Bystrack 1981). BBS data provide an index of population abundance at the scale of an

2   individual route that can be used to estimate trends in relative abundance at various geographic

3   scales. We selected bird species that were present in more than 10% and fewer than 80% of

4   sampling sites in the study system during the selected time periods (to avoid extremely common

5   and extremely rare species), excluding species whose distributions mainly occur outside the

6   study region and those for which the region may not contain environmental limits respectively.

7   Aquatic and coastal bird species were also excluded because we did not expect the terrestrial-

8   based BBS routes to sample breeding populations of these species effectively. In total, 132

9   species satisfied the criteria for analyses.

10   We used BBS data from 1970 (earliest year when enough routes were available for

11   analysis) to 2002, over which period sufficiently high-resolution climate data were available to

12   match route locations. To reduce sampling variation in abundance caused by observer and

13   interannual weather effects, we considered two alternate five-year windows representing an

14   early (1970-74) and a later period (1998-2002). A given species was considered to be 'present'

15   on a particular transect route if it was recorded there in one or more of the five years. To avoid

16   possible 'false zeroes' in species counts, we only included routes that were sampled in all years

17   during each period (1970-74 and 1998-2002). Abundance was the average number counted on

18   a route over the five-year period. This approach has been adopted in previous studies on species

19   distributions that use BBS data (Hitch & Leberg, 2007; Philips *et al*., 2010). Finally, we also

20   excluded from analyses those routes that were so close to the ocean that their centroids were

21   located in the water, which would bias estimates of terrestrial climate. This initial screening

22   resulted in a dataset of 642 routes, of which 332 and 541 routes were sampled in the early and

23   later time periods respectively, with 231 sampled in both periods (Fig. 1).

24   **Environmental data**

1   We obtained historical climate data generated by the Parameter Regression of Independent

2   Slope Model (PRISM) (Oregon Climate Service, Corvallis, Oregon, USA) for the continental

3   United States (Daly *et al*., 2002). Equivalent data for Canada were provided by the Canadian

4   Forest Service, Natural Resources Canada (http://cfs.nrcan.gc.ca). Both climate datasets were

5   created using point meteorological station data, digital elevation models, and other spatial data

6   sets to generate interpolated gridded estimates of monthly, yearly, and event-based climatic

7   parameters, such as precipitation, temperature, and dew point. We used maps at a spatial

8   resolution of 2.5-arcmin (approximately 3 km cell size at this latitude) (Daly *et al*., 2000). For

9   the 30-arcsec resolution British Columbia data, we resampled to 2.5-arcmin to match the

10   resolution of the PRISM data.

11   We selected a set of seven climatic variables previously reported to be associated with

12   bird species distributions, reflecting conditions in the breeding season and during summer and

13   winter months when the most extreme conditions are likely to be experienced (Green *et al*.

14   2008; Jiménez-Valverde *et al*., 2011). The seven climatic predictors included in the models

15   were: average daily maximum temperature of the hottest month in the study system (July),

16   average daily minimum temperature of coldest month (January) and total precipitation of

17   wettest (December) and driest month (July). The peak breeding period for most birds in the

18   study region was in June, so we also considered maximum temperature, minimum temperature

19   and precipitation for this month. The full set of predictor variables included in the analyses is

20   listed in Table 1.

21   We summarized all climate variables within 1 km of BBS routes, the maximum distance

22   within which birds are likely to be detected in a survey (Betts *et al*., 2007), taking the average

23   condition for each climate variable across the five years in each period. Distribution models

24   could fail if there is a mismatch between the spatial resolution of population processes and of

25   the environmental predictor variables (Araújo & Peterson, 2012). It has frequently been noted

1   that the spatial scale of studies strongly affects relative importance of environmental factors

2   associated with species distributions (Johnson *et al*., 2004; Olivier & Wotherspoon, 2005;

3   Jiménez-Valverde *et al*., 2011). In this particular case, missing the appropriate spatial scale of

4   the study species may lead to incorrect interpretation of the results (Beale *et al*., 2008). We

5   therefore repeated analyses using climatic conditions within 20 and 50 km of each route, to

6   represent the sub-regional or regional scales that have previously been related to bird

7   populations (Tittler *et al*., 2006). However, model performance was highly correlated across

8   the three spatial scales ($R^2 > 0.8$ in all cases) so we report only the 1 km buffer model

9   performance here.

10

11   **Statistical analyses**

12   *Model Development*

13   Models were developed using the 'gbm' package in R (R Development Core Team, 2010) for

14   Boosted Regression Trees analyses, which have been widely used for climatic envelope models

15   (Randin *et al*., 2009; Carvalho *et al*., 2010; Verburg *et al*., 2011; Engler *et al*., 2011). Boosted

16   Regression Trees (BRTs) are a type of machine-learning method that combines the strength of

17   regression trees and boosting; that aims to fit a single parsimonious model. GBMs combine

18   many simple models to give improved predictive performance and provide the capacity to

19   include different types of predictor variables and to accommodate missing data. BRTs exhibit

20   high prediction performance while minimizing the risks of overfitting (Elith *et al*., 2006). In

21   addition, they are sufficiently flexible to include nonlinear relationships and interactions

22   between predictors (Elith *et al*., 2008). We generate BRT models with the set of seven climatic

23   variables as predictors and observed occurrence or abundance for each time period as response

24   variables (Fig. 2). Both abundance and occurrence models such as ours are well known to suffer

1   from potential biases caused by imperfect detection (MacKenzie *et al*. 2003, Kery 2011).

2   However, we elected not to account for detection in our modeling strategy for four reasons.

3   First, BBS data are not collected using the repeated temporal sample structure required for

4   occupancy modeling (MacKenzie *et al*. 2003). Second, to date, no machine learning methods

5   (e.g., BRT) exist that account for imperfect detection. Machine learning methods such as BRT

6   enable the fitting of complex structures (non-linearities, interactions) that would be extremely

7   computationally challenging in an occupancy framework. Thirdly, 'occupancy', after

8   accounting for imperfect detection, is a latent variable and therefore impossible to validate on

9   independent data because the 'true' state of independent data are unknown (Welsh *et al*. 2013).

10   Finally, as our primary objective was SDM validation, and the same search effort was applied

11   to every transect in both time periods, this approach was therefore inappropriate.

12

13   *Model evaluation*

14   We evaluated both abundance and distribution models in two ways: (1) description of the fit of

15   the original models within a given time period (verification) and (2) model forecasting and

16   hindcasting with independent data, in our case using models developed during one time period

17   to predict observed patterns in the other period (cross-validation; Araújo & Guisan 2006;

18   Dobrowsky *et al*., 2011). Given the data (continuous *versus* binary) and observed patterns (lack

19   of normality in abundance data), the procedures for verification and cross-validation depended

20   on the distribution of response variables. We verified the models using data from the same time

21   period used for model development. We calculated the performance of the presence/absence

22   models using AUC (area under the receiving operating characteristic curve) (Fielding & Bell

23   1997; Manel *et al*., 2001; McPherson *et al*., 2004). Values normally range from 0.5 (no better

24   than random association) to 1 (perfect fit). There is no universally accepted ideal measure of

25   model performance, but AUC has been widely used (but see Lobo *et al*. 2008) as a threshold

1   independent metric of model fit and its properties are well understood (Thuiller, 2003; Araújo

2   *et al*., 2005; Brotons *et al*., 2007; Pearman *et al*., 2008; Gutiérrez Illan *et al*., 2010) (Fig S2). We

3   evaluated abundance models using Spearman's rank correlation coefficients (Spearman´s ρ)

4   between predicted (from model-averaged coefficients) against observed abundance values (Fig.

5   2). We used rank correlations coefficients (ρ) between predicted and observed abundance

6   values because observed count numbers were low for almost all species on some routes (leading

7   to deviations from normality), and for consistency with the analysis of abundance changes

8   between periods (some species showed non-linear relationships between predicted and

9   observed abundance changes, e.g. Fig 5). We also tested for correlations between observed and

10   predicted abundance using Pearson's r, but results were not substantively different, so here we

11   report only Spearman ρ , which is a more conservative test.

12   For cross-validation, we used the models developed in one time period and then used

13   climate data in the other period to predict occurrences or abundance of the selected species in

14   the target routes (Fig. 2). These were compared with the observed measures of occurrence and

15   abundance in the alternative test period. As an additional, more challenging test of the efficacy

16   of climate envelope models, we used our models to make forecast and hindcast predictions

17   about occurrence and abundance at routes that were not sampled in the alternative time-period.

18   We ran the models based on the whole set of routes in each period (332 in 1970-74 and 541 in

19   1998-02) and evaluated their predictive power with the set of routes that were not sampled in

20   the alternate period (101 in 1970-74 and 309 in 1998-02). These tests were thus carried out on

21   both spatially and temporally independent data (Bahn & McGill, 2013).

22

23   *Predicting Species Distributions and Abundances Over Time*

1   The strongest test of whether the climate variables in (spatial) models are causally linked to

2   species' distributions and abundances is to make predictions about changes over time, and then

3   to test these against observed changes. First, we carried out these analyses using changes in

4   occupancy through time. A given species at a sampling location can (i) colonize, (ii) go locally

5   extinct, (iii) persist, or (iv) remain absent during a given period of time (Nichols *et al*., 1998;

6   MacKenzie *et al*., 2003). Thus, we identified the routes where each of these states had been

7   observed (changes in occupancy: absence to presence of *n* individuals, and *vice versa*). We only

8   considered the subset of routes monitored in both time periods to ensure data consistency. The

9   total number of routes that were sampled in both years and therefore included in the analyses

10   was 231 (out of 332 in 1970-74 and 541 in 98-02). Out of the 132 target species in our study

11   system, we selected for analysis the species for which local extinction or colonization had

12   occurred for >5 routes over the study period.

13   To estimate expected change in occupancy, we ran BRTs using data from the first time

14   period to estimate initial occupancy probability $(\widehat{\Psi}_{t1})$. We then predicted to the second period

15   using this first model given changes in climate that occurred on each route $(\widehat{\Psi}_{t2})$. The

16   difference between these values $(\widehat{\Psi}_{t2} - \widehat{\Psi}_{t1})$ was considered the expected change in probability

17   of occupancy $(\Delta\Psi)$. Prediction accuracy was assessed by comparing $\Delta\Psi$ with observed change

18   in occupancy status (Fig 4). We used a paired t-test (98 species) to investigate whether observed

19   change in occupancy (a dichotomous response variable; locally extinct versus locally colonized

20   sites) was significantly associated with the predicted change in occupancy (a continuous

21   variable).

22   In the case of the abundance models, which incorporate both abundance changes (on

23   routes populated in both periods) *and* changes in occupancy (absence to presence of *n*

24   individuals, and *vice versa*) we followed a similar procedure. To calculate abundance changes,

1   we used the 1970-74 model to describe initial abundances in the first time period ($\hat{\eta}_{t1}$) for each

2   route. We projected abundance in the second time period ($\hat{\eta}_{t2}$) using the t1 model parameterized

3   with t2 climate data. The difference ($\Delta\eta$) represents the expected change in abundance on each

4   route ($\hat{\eta}_{t2} - \hat{\eta}_{t1}$). We then tested the correlation between $\Delta\eta$ and observed abundance changes.

5   Transect routes where a species was absent in both time periods were excluded to avoid the

6   possibility that statistical fits might be exaggerated (large numbers of points with near-zero

7   predicted change and zero change observed). Again, we only considered the subset of routes

8   monitored in both time periods. A total of 132 species satisfied criteria for analysis of

9   abundance changes. We assessed predictive power by calculating Spearman rank correlations

10   (ρ), given that the relationships between predicted and observed abundance changes were not

11   always linear (Fig. 5), with no single transformation proving suitable for all species. For brevity,

12   we report only forecast results for both occupancy and abundance change models. Backcast

13   prediction accuracies were slightly higher and qualitatively similar. A summary of the complete

14   model building/cross-validation process is shown in Figure 2.

15

16   *Relative contribution of climate variables*

17   We calculated the relative influence of each predictor in BRTs using the gbm package; this

18   provides a measure of the strength of each variable's influence on the total response and is

19   reflected as a proportion (Elith *et al*., 2008). We recorded the top-ranked explanatory variable

20   for each species, as well as the three top-ranked variables. For each variable, we counted the

21   number of species for which its independent contribution was ranked first, or within the top

22   three (Radford & Bennett, 2007), thus providing an overall estimate of the importance of each

23   variable to bird distributions and abundances in the region. As a further test, we also calculated

1   the relative contribution of the variables for the species with the best-performing models (34

2   species with Spearman´s ρ above 0.4).

3

4   *Spatial autocorrelation*

5   One of the most common criticisms of the species distribution models is spatial autocorrelation

6   of results, which could lead to spurious relationships and thus, to infer wrong conclusions

7   (Beale *et al*., 2008). Spatial autocorrelation can influence the reliability of biogeographic

8   analyses, particularly based on sample sites separated by short geographic distances (Algar *et*

9   *al*., 2009). We tested for spatial autocorrelation in residuals of both presence-absence and

10   abundance models using correlograms (Moran´s *I*; Fortin *et al*., 1989, Betts *et al*., 2006).

11

12   **RESULTS**

13   *Climatic trends*

14   Although temperatures predominantly warmed from 1970-74 to 1998-2002, both changes in

15   temperature and precipitation showed a spatially patchy pattern (Fig. 1, Table 1). This spatial

16   heterogeneity in temperature and precipitation changes provides useful variation to assess

17   occupancy and population changes in response to variation in the climate.

18   *Model verification*

19   Distribution models generally performed well for most species within both time periods

20   (internal validation). For presence/absence models, 87% (1970-74) and 80% of species (1998-

21   02) showed AUC values >0.8, with mean (±SE) AUCs of 0.88 ± 0.01 and 0.87 ± 0.01 for the

22   two periods respectively (Fig. 3) (Fig S2). Correlations between observed and predicted

1   abundance were also quite high when tested within time periods; Average ρ (±se) was 0.47 ±

2   0.02 for 1970-74 (94% of species showing significant associations; p<0.01) and 0.49 ± 0.01 for

3   1998-2002 (98% of species showing significant associations; p<0.01; Fig. 3).

4   *Model cross-validation between time periods*

5   Prediction success was lower in validation than in verification, though not substantially. When

6   forecasting using presence/absence models, mean (±SE) AUC was 0.77 ± 0.01. When

7   hindcasting, mean (±SE) AUC value was 0.81 ± 0.02 for presence/absence models (Fig. 3). In

8   total, 40% (forecasting) and 59% (hindcasting) of the species showed excellent (AUC > 0.8)

9   predictive performance between time periods. In abundance models, forecast results were

10   positively correlated with observed abundance in the second time period (mean $\rho = 0.34 \pm 0.02$

11   (90 % out of 132 species significant at p<0.01)). Hindcast results yielded slightly higher

12   correlations between observed and predicted abundances ($\rho = 0.38 \pm 0.02$ (92 % out of 132

13   species significant with p<0.01)) (Fig. 3). Abundance models for 61% and 72% of species (for

14   forecasting and hindcasting, respectively) showed correlations $\rho > 0.3$. For each analysis, the

15   improved performance of hindcast predictions is likely to reflect the higher number of routes

16   available for model building in the later period.

17   Performance of the abundance models (Spearman ρ) were significantly correlated with

18   those of the presence/absence models (AUC) in both periods (Spearman $\rho = 0.59$ (70-74

19   models); Spearman $\rho = 0.68$ (98-02 models). $N = 132$ in both cases), suggesting common drivers

20   of abundance and distributions. Results obtained in verification and cross-validation for the full

21   set of target species are shown in table S1. To test the sensitivity of our results to the statistical

22   model, we also applied stepwise logistic regressions to generate climate-envelope models for

23   both presence/absence and abundance. These gave very similar results in making predictions

1   between time periods, but the AUC when using Boosted Regression Trees was higher for 95%

2   of species (Fig. S1).

3   *Testing changes in bird occupancy and abundance through time*

4   We tested the capacity of models to predict occupancy changes through time for 98 species that

5   satisfied criteria for analyses (Fig. 4). Mean change in predicted suitability of colonized routes

6   was significantly higher, i.e. more positive, than for routes that went locally extinct (paired t-

7   test, t=3.094; *P*<0.005; N=98). However, results varied widely across species (Fig. 4). In

8   general, models predicted local extinctions better than the local colonisations. Average climate

9   suitability decreased over time in the routes for seventy of the 98 species which went locally

10 extinct. Average climate suitability increased in colonized routes for 52 species (Fig 4).

11   In predicting changes in abundance over time, 71 out of 132 species showed significant

12 correlations between observed and predicted changes (mean $\rho = 0.28 \pm 0.02$, across all species).

13 Again, model quality varied widely, with 61 species (46%) showing weak predictive power (ρ

14 < 0.2), 24 species (18%) showing some level of predictive power ($0.2 > \rho < 0.5$) and 47 species

15 (36%) showing correlations >0.5 (Fig. 5b). Model performance for one high-performance and

16 one medium-performance example species are shown in Figure 5. The purple finch

17 (*Haemorhous purpureus*) represents a species with a typical northern distribution in North

18 America, whereas loggerhead shrike (*Lanius ludovicianus*) has a typical southern distribution.

19 For both species, there is some indication that climate-related declines are better predicted than

20 increases (Fig. 5). This is consistent with the results obtained in the occupancy change models

21 where models tended to better predict extinctions than colonizations.

22   The residuals of abundance models were not spatially autocorrelated for the majority of

23 the species. Ninety-five species showed no significant (*p*>0.05) autocorrelation at any distance

24 classes. Furthermore, only 12 out of 132 species showed Moran´s *I* >0.2 at any spatial lag,

1   which is generally considered to reflect strong spatial autocorrelation (see full results in Table

2   S2, detailed plots for exemplar species in Fig. S3) (Lichstein *et al*. 2002).

3

4   *Relative contribution of climate variables*

5   Overall, precipitation was a more important predictor than temperature in both distribution and

6   abundance models (Fig. 6). This conclusion held whether we considered the single top variable

7   in each species' model, or whether a variable was one of the three top predictors (Fig. 6). Fig

8   6b shows very similar results obtained when considering only the 34 species with evaluation

9   coefficients (Spearman´s ρ) above 0.4. Precipitation in the wettest month (December) was

10   particularly important, with additional contributions from June and July precipitation (Fig. 6).

11   January temperature was, on average, the most important temperature variable included in our

12   models. Hence, the abundance changes that could be predicted by the models were mainly

13   driven by spatio-temporal changes in precipitation and warming trends in winter temperature

14   over time.

15

16   **DISCUSSION**

17   Our results show that climate envelope models had considerable capacity for describing the

18   abundance and distribution of bird species in western North America. This is consistent with

19   previous studies showing high predictive ability for distribution models that are trained and

20   tested in the same time period (La Sorte & Jetz, 2012, Renwick *et al*. 2012, Foden *et al*. 2013,

21   Smith *et al*. 2013). Further, our models generally performed well at predicting both occupancy

22   and abundance in alternative time periods (transferability). This is perhaps not surprising given

23   the relatively short time-period over which our models predicted (32 years); one would expect

1   there to be temporal autocorrelation in bird distributions, explained partly by an inertia in the

2   distribution of the plant species and climatic envelopes on which they depend (Araújo *et al*.

3   2005, Botkin *et al*. 2007, Rapacciuolo *et al*. 2013; Watling *et al*. 2013).

4   More telling was our finding that, for some species, climate envelope models were also

5   capable of predicting abundance and occupancy *changes* across the western portion of the

6   continent; 54% of the species we examined showed significant correlations between predicted

7   and observed abundance changes. Though these models are still correlative, they substantially

8   reduce two problems in climate envelope model validation: (1) they are free from problems of

9   temporal autocorrelation in model predictions that would lead to high quality models based

10   solely on the tendency of species to remain at certain population levels or distributions over

11   short time periods (Araújo *et al*., 2005, Rapacciuolo *et al*., 2013); (2) they are less likely than

12   static models to be confounded with biotic variables that show similar distributions to climate;

13   for example, birds are known to be strongly associated with vegetation structure and

14   composition (MacArthur & MacArthur, 1961). Our finding that changes in bird abundance and

15   occupancy are predicted by climate provides stronger evidence that climate itself is an

16   important role as a driver of bird populations – even over relatively short temporal scales. This

17   role may be direct (via thermal limitations; *sensu* Jankowski *et al*., 2013) or indirect –

18   propagated through influences to, for example, the phenology of vegetation and/or food

19   availability (Both *et al*., 2006).

20   Model prediction success is expected to decline as one moves from verification (testing

21   against the data used to build the model), to cross-validation (testing against observed patterns

22   in another time period) and temporal prediction (changes in abundance patterns in space and

23   time) (Araújo *et al*., 2005). Our models support this expectation; abundance models trained

24   and tested in 1970-74 (i.e., verification) showed high concordance with observed data ($\rho=0.47$).

25   In cross-validation to a new time period, correlations dropped ($\rho=0.34$) and then declined

1   further when predicting geographical patterns of abundance changes across time periods

2   (ρ=0.28). Nonetheless, predictions of temporal changes in abundance patterns were strong

3   (ρ>0.5) for over a third of the species.

4   Though still scarce, a number of recent studies have tested for the transferability of

5   climate envelope models in space and time for mammals (Rubidge *et al*., 2012), plants

6   (Pearman *et al*., 2008), insects (Kharouba *et al*., 2009) and birds (Rapacciuolo *et al*., 2013;

7   Johnston *et al.* 2013). Superficially, the degree of climate envelope model success appears to

8   vary widely across studies and taxa, but much of this variability is accounted for by whether or

9   not studies attempted to model occupancy change, or simply model transferability. Generally,

10   studies that built models in time t_1 and predict distributions in t_2 report optimistic results

11   (Dobrowski *et al*., 2011, Watling *et al*., 2013). In contrast, Rapacciuolo *et al*. (2013) recently

12   found that although climate envelope models for plants, birds and butterflies did well at

13   predicting distributions (transferability was high), performance was poor when they attempted

14   to predict changes in occupancy status at range edges. Our findings support this result for a

15   substantial number of species (61/132, 48% of models showed correlations <0.2). These results

16   provide an important cautionary note: for some species, high explanatory power on temporally-

17   independent records does not necessarily indicate a model's ability to predict changes through

18   time. However, the rest of the species we considered showed significant, and in some cases

19   strong, correlations between observed and predicted abundance changes.

20   One possible explanation for the higher agreement between predicted and observed

21   abundance changes in our study in relation to Rapacciuolo *et al*. (2013) lies in the order of

22   magnitude greater geographical scale of our study (2,308,000 km² versus 229,848 km²). This

23   permitted us to encompass the full latitudinal extent of many species' ranges. Several studies

24   have shown that it is particularly important to include the complete species' environmental

25   range to achieve more accurate predictions (Pearson *et al*., 2002; Thuiller *et al*., 2004; Barbet-

1   Massin *et al*., 2010) and that missing the climatic limits of the species is more likely lead to the

2   conclusion that distributions of species are not determined by climate (Beale *et al*., 2008). Our

3   study is one of the first to demonstrate that climate envelope models predict species

4   distributions and abundances in new, independent locations (see Rubidge *et al*., 2012).

5   Though the majority of our models predicting occupancy and abundance changes were

6   significantly correlated with observed changes, for most species substantial variation remained

7   unexplained. It is well known that a wide range of non-climatic factors drive biodiversity

8   responses – many of which remain challenging to incorporate into SDMs. First, land-use

9   change has clear potential to limit the efficiency with which even fairly vagile species can 'keep

10 pace' with climate change (Jetz *et al*., 2007). Highly fragmented habitat distributions may

11 preclude dispersal to patches that have newly emerged as part of a species' fundamental niche

12 (Opdam & Wascher, 2004). Few efforts to date have quantitatively examined the degree to

13 which land-use change interacts with climate to drive distributions (Luoto *et al*., 2007). Second,

14 biotic relationships (e.g., competition, predation, mutualism) all play a role in driving

15 distributions (Blois *et al*., 2013). Though new techniques are emerging to explicitly incorporate

16 such biotic factors (Heikkinen *et al*., 2007), these have not been extensively validated to

17 determine the degree to which they improve model predictions over longer time periods (but

18 see Rubidge *et al*., 2012). Third, the spatial resolution of most climatic envelope models tends

19 to be in the order of 1-100 km^2 – a scale which is likely mis-matched with the scale of perception

20 by many organisms (Gillingham *et al*., 2012), including birds. A number of studies have

21 recently acknowledged that fine-scale variability in thermal and precipitation regimes have the

22 potential to provide 'refugia' or 'buffering' against landscape or regional trends in climate

23 (Dobrowski, 2011; Moritz & Agudo, 2013). Unfortunately, long-term data on animal

24 distributions, including the data used in this study, are rarely collected at sufficiently fine spatial

25 resolutions to allow for modelling (let alone validating) such microclimatic effects.

1   Nevertheless, it is important to note that despite these additional sources of variation, climate

2   variables alone successfully predicted both abundance and distributional changes for many of

3   the species we examined. We expect that new efforts to incorporate physiological tolerances

4   (Jankowski *et al*., 2013), dispersal behaviour (LaSorte & Jetz, 2010), and fine-scale landcover

5   data (Shirley *et al*., 2013) will improve upon the models we report here.

6   An additional source of variation may arise from the nature of the count data analysed.

7   Though quantifying abundance using 5-year 'windows' undoubtedly increased detections, and

8   hence noise relating to detectability, the lack of within-year repeat counts in BBS data precludes

9   accounting statistically for biases relating to imperfect detection (MacKenzie *et al*. 2003).

10   Nevertheless, it is highly unlikely that imperfect detection biased our results *in favour* of SDMs

11   that validate well on independent data.

12   Most studies of how climate change alters the distributions of species have emphasised

13   the effects of temperature (Walther *et al*., 2002; Thomas *et al*., 2004; Chen *et al*., 2011), but it

14   has been argued that precipitation could exert an equally important role for some organisms

15   (Tingley *et al*., 2012). In our study, with the exception of minimum January temperature, the

16   three precipitation variables featured more strongly in models than did the remaining

17   temperature variables for most species (Fig. 6). Our study thus confirms the importance of

18   considering precipitation in future projections of species under climate change. We hypothesize

19   that precipitation is an important determinant of range retreats in northern species that

20   experience increased desiccation of their habitats in the south, and may facilitate the expansion

21   of drought-tolerant species from the south. However, precipitation change is complex in

22   mountainous terrain (Fig. 1), which has resulted in complex patterns of predicted and observed

23   geographic patterns of abundance change (Fig. 5). Hence, different species may be shifting

24   their distributions in quite variable directions; a single species even may show variation in the

1   direction of shifts in different regions, depending on which environmental variables are limiting

2   and the degree to which they are changing (Root & Schneider, 1993; Root *et al.*, 2003).

3   Interestingly, winter conditions (precipitation in the wettest month, December, and

4   temperature in the coldest month, January) were the most important predictor variables for most

5   species. For resident species, this may reflect overwinter physiological stress and food

6   availability which in turn affects survival (Robinson *et al.*, 2007, Doherty & Grubb, 2002), but

7   for migrants that are absent during these periods, such changes likely reflect lagged climate

8   effects. For instance, warmer winter temperatures would affect rates of snowmelt, which in turn

9   influences moisture availability and therefore ecosystem productivity during the summer

10 months. Moreover, moisture storage carryover also affects air temperature through latent heat

11 exchanges (Porporato *et al.*, 2004; Nolin & Daly, 2006).

12   The predictive power of climate envelope models for birds exhibited variable success

13 across species, but declined as data independence increased. Nevertheless, we provide evidence

14 that climate envelope models are capable of predicting abundance changes through time for a

15 third to half of species, suggesting that climate is driving the changes. Over the 32-year period

16 considered, precipitation was a major determinant of geographic-scale changes in the

17 abundance patterns of terrestrial bird species in western North America. Our results for birds

18 could therefore be considered a 'best case' scenario with respect to the transferability of climate

19 envelope models because of their relatively high dispersal abilities, and other taxa might show

20 lower prediction success due to lags in dispersal (Ko *et al.*, 2011). However, climate is a better

21 predictor of decreases and, ultimately, of local extinctions in our study, than it is of increases

22 and local colonizations, and hence the predictive power of our models does not rely on strong

23 dispersal. In conclusion, our ability to predict geographic patterns of abundance change through

24 time demonstrates the importance of climate, particularly precipitation, to the changing

25 distributions of a third to a half of the species studied, but the variation explained also implies

1   that factors other than climate, such as dispersal, land-use and heterospecifics are also important

2   determinants of large-scale distribution change. The quest for improved model predictions will

3   inevitably involve trade-offs between limited extent of fine-resolution data depicting

4   organism´s responses to land use/land cover and biotic interactions (which produce detailed,

5   accurate models of local places that are hard thus problematic to generalize) and the desire to

6   create broad-scale models that are relevant to understanding global change.

7

8   **ACKNOWLEDGEMENTS**

22

1   **REFERENCES**

2   Algar AC, Kharouba HM, Young ER, Kerr JT (2009) Predicting the future of species diversity:

3   macroecological theory, climate change, and direct tests of alternative forecasting methods.

4   Ecography, 32, 22-33.

5   Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling.

6   Journal of Biogeography, 33, 1677-1688.

7   Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact

8   models under climate change. Global Change Biology, 11, 1504–1513.

9   Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling.

10   Ecology, 93, 1527–1539.

11   Bahn V, McGill BJ (2013) Testing the predictive performance of distribution models. Oikos,

12   122, 321-331.

13   Bale JS, Masters GJ, Hodkinson ID et al (2002) Herbivory in global climate change research:

14   direct effects of rising temperature on insect herbivores. Global Change Biology, 8, 1–16.

15   Barbet-Massin M, Thuiller W, Jiguet F (2010) How much do we overestimate future local

16   extinction rates when restricting the range of occurrence data in climate suitability models?

17   Ecography, 33, 878-886.

18   Beale CM, Lennon JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale

19   associations with climate in European birds. Proceedings of the National Academy of

20   Sciences USA, 105, 14908-14912.

1   Beale CM. Baker NE, Brewer MJ, Lennon JJ (2013) Protected area networks and savannah

2   bird biodiversity in the face of climate change and land degradation. Ecology Letters, 16,

3   1061-1068.

4   Betts MG, Diamond AW, Forbes GJ, Villardd MA, Gunn JS (2006) The importance of spatial

5   autocorrelation, extent and resolution in predicting forest bird occurrence. Ecological

6   Modelling, 191, 197-224.

7   Betts MG, Forbes GJ, Diamond AW (2007) Thresholds in songbird occurrence in relation to

8   landscape structure. Conservation Biology, 21, 1046-1058.

9   Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate Change and the past,

10   present, and future of biotic interactions. Science, 341, 499-504.

11   Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines

12   in a long-distance migratory bird. Nature, 441, 81-83.

13   Botkin DB, Saxe H, Araújo MB et al (2007) Forecasting the effects of Global Warming on

14   biodiversity. BioScience, 57, 227-236.

15   Brotons L, Herrando S, Pla M (2007) Updating bird species distribution at large spatial scales:

16   applications of habitat modelling to data from long-term monitoring programs. Diversity and

17   Distributions, 13, 276-288.

18   Bystrack D (1981) The North American breeding bird survey. Studies in Avian Biology, 6,

19   34-41.

20   Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to

21   actions – conserving vulnerable animal groups in hotspots at a regional scale. Global Change

22   Biology, 16, 3257-3270.

1   Cayan, DR (1996) Interannual climate variability and snowpack in the western United States.

2   Journal of Climate, 9, 928–948.

3   Chamaille-Jammes S, Fritz H, Murindagomo F (2006) Spatial patterns of the NDVI-rainfall

4   relationship at the seasonal and interannual time scales in an African savanna. International

5   Journal of Remote Sensing, 27, 5185-5200.

6   Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species

7   associated with high levels of climate warming. Science, 333, 1024-1026.

8   Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou J, Mynsberge (2011) Changes in

9   climatic water balance drive downhill shifts in plant species' optimum elevations. Science,

10   331, 324-327.

11   Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P (2002) A knowledge-based approach

12   to the statistical mapping of climate. Climate Research, 22, 99-113.

13   Daly C, Taylor GH , Gibson WP, Parzybok TW, Johnson GL , Pasteris PA (2000)

14   Transactions of the American Society of Agricultural Engineers, 43.

15   Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not

16   fast enough. Proceedings of the Royal Society B, 275, 2743-2748.

17   Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate.

18   Global Change Biology, 17, 1022-1035.

19   Dobrowski SZ, Thorne JH, Greenberg JA, Safford HD, Mynsberge AR, Crimmins SM,

20   Swanson AK (2011) Modeling plant distributions over 75 years of measured climate change

21   in California, USA: relating temporal transferability to species traits. Ecological Monographs,

22   81, 241–257.

1   Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented

2   forested landscape. Ecology, 83, 844-857.

3   Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species'

4   distributions from occurrence data. Ecography, 29, 129–151.

5   Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. Journal

6   of Animal Ecology, 77, 802–813.

7   Engler R, Randin CF, Thuiller W et al (2011) 21st century climate change threatens mountain

8   flora unequally across Europe. Global Change Biology, 17, 2330–2341.

9   Fielding AH & Bell JF (1997) A review of methods for the assessment of prediction errors in

10   conservation presence/absence models. Environmental Conservation, 1, 38-49.

11   Foden W, Midgley GF, Hughes G et al (2007) A changing climate is eroding the geographical

12   range of the Namib Desert tree Aloe through population declines and dispersal lags. Diversity

13   and Distributions, 13, 645–653.

14   Foden WB, Butchart SH, Stuart SN, et al. (2013) Identifying the world's most Climate

15   Change vulnerable species: A systematic trait-based assessment of all birds, amphibians and

16   corals. PLOS ONE 8, e65427.

17   Fortin MJ, Drapeau P, Legendre P (1989) Spatial autocorrelation and sampling design in plant

18   ecology. Vegetatio, 83, 209-222.

19   Gaston, K (2003) The structure and dynamics of geographic ranges. Oxford University Press,

20   Oxford.

1   Gillingham PK, Palmer SCF, Huntley B, Kunin WE, Chipperfield JD, Thomas CD (2012)

2   The relative importance of climate and habitat in determining the distributions of species at

3   different spatial scales: a case study with ground beetles in Great Britain. Ecography, 35, 831-

4   838.

5   Green R, Collingham YC, Willis SG, Gregory RD, Smith KW, Huntley B (2008)

6   Performance of climate envelope models in retrodicting recent changes in bird population size

7   from observed climatic change. Biology Letters, 23, 599-602.

8   Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology.

9   Ecological Modelling, 135, 147-186.

10   Gutiérrez Illán J, Gutiérrez D, Wilson RJ (2010) The contributions of topoclimate and land

11   cover to species distributions and abundance: fine-resolution tests for a mountain butterfly

12   fauna. Global Ecology and Biogeography, 19, 159-173.

13   Hamlet AF, Mote PW, Clark MP, Lettenmaier DP (2007) Twentieth-century trends in runoff,

14   evapotranspiration, and soil moisture in the Western United States. Journal of Climate, 20,

15   1468–1486.

16   Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Körber JH (2007) Biotic interactions

17   improve prediction of boreal bird distributions at macro-scales. Global Ecology and

18   Biogeography, 16, 754-763.

19   Heim RR (2002) A Review of twentieth-century drought indices used in the United States.

20   Bulletin of the American Meteorological Society, 83, 1149–1165.

21   Hitch AT, Leberg PL (2007) Breeding distributions of North American bird species Moving

22   north as a result of Climate Change. Conservation Biology, 21, 534–539.

1 Huntley B, Spicer RA, Chaloner WG, Jarzembowski EA (1993) The use of climate response

2 surfaces to reconstruct palaeoclimate from quaternary pollen and plant macrofossil data [and

3 discussion]. Philosophical Transactions of the Royal Society B: Biological Sciences, 1297,

4 215-224.

5 Hutchinson GE (1957) The multivariate niche. Cold Spring Harbor Symposia on Quantitative

6 Biology. Vol. 22, 415-421.

7 Jankowski JE, Londoño GA, Robinson SK, Chappell MA (2013) Exploring the role of

8 physiology and biotic interactions in determining elevational ranges of tropical animals.

9 Ecography, 36, 001-012.

10 Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on

11 the global diversity of birds. PLoS Biol 5, e157.

12 Jiménez-Valverde A, Barve N, Lira-Noriega A et al (2011) Dominant climate influences on

13 North American bird distributions. Global Ecology and Biogeography. 20, 114-118.

14 Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning:

15 using resource selection functions to map the distribution of mountain caribou at multiple

16 spatial scales. Journal of Applied Ecology, 41, 238–251.

17 Johnston A, Ausden M, Dodd AM et al. (2013) Observed and predicted effects of climate

18 change on species abundance in protected areas. Nature Climate Change, 3, 1055-1061.

19 Kery M (2011) Towards the modelling of true species distributions. Journal of Biogeography,

20 38, 617–618.

21 Kharouba HM, Algar AC, Kerr JT (2009) Historically calibrated predictions of butterfly

22 species' range shift using global change as a pseudo-experiment. Ecology, 90, 2213–2222.

1   Ko CY, Root TL, Lee PF (2011) Movement distances enhance validity of predictive models.

2   Ecological Modelling, 222, 947-954.

3   La Sorte FA, Jetz W (2010) Avian distributions under climate change: towards improved

4   projections. Journal of Experimental Biology, 213, 862-869.

5   La Sorte FA, Jetz W (2012) Tracking of climatic niche boundaries under recent climate

6   change. Journal of Animal Ecology, 81, 914–925.

7   Lawler JJ, Wiersma YF, Huettmann F (2011) Using species distribution models for

8   conservation planning and ecological forecasting. In: *Predictive Species and Habitat*

9   *Modeling in Landscape Ecology*, 271-290.

10   Lichstein JW, Simons TR, Shriner SA, Franzreb KE (2002) Spatial autocorrelation and

11   autoregressive models in ecology. Ecological Monographs, 72, 445–463.

12   Lobo, J. M., A. Jimenez-Valverde, and R. Real (2008) AUC: a misleading measure of the

13   performance of predictive distribution models. Global Ecology and Biogeography, 17, 145-

14   151.

15   Luoto M, Virkkala R, Heikkinen RK (2007) The role of land cover in bioclimatic models

16   depends on spatial resolution. Global Ecology and Biogeography, 16, 34-42.

17   MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology, 42, 594-598.

18   MacKenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB (2003) Estimating site

19   occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology,

20   84, 2200-2207.

1   Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence–absence models in ecology:

2   the need to account for prevalence. Journal of Applied Ecology, 38, 921–931.

3   Mcpherson JM, Jetz W, Rogers DJ (2004) The effects of species' range sizes on the accuracy

4   of distribution models: ecological phenomenon or statistical artefact? Journal of Applied

5   Ecology, 41, 811–823.

6   Moritz C, Agudo R (2013) The future of species under climate change: Resilience or Decline?

7   Science, 341, 504-508.

8   Nichols JD, Boulinier T, Hines JE, Pollock KH, Sauer JR (1998) Estimating rates of local

9   species extinction, colonization, and turnover in animal communities. Ecological

10   Applications, 8, 1213–1225.

11   Nolin AW, Daly C (2006) Mapping "At Risk" Snow in the Pacific Northwest. Journal

12   Hydrometeorology, 7, 1164-1171.

13   Ohlemüller R, Huntley B, Normand S, Svenning JC (2012) Potential source and sink

14   locations for climate-driven species range shifts in Europe since the last glacial maximum.

15   Global Ecology and Biogeography, 21, 152-163.

16   Oliver TH, Gillings S, Girardello M et al. (2012) Population density but not stability can be

17   predicted from species distribution models. Journal of Applied Ecology, 49, 581–590.

18   Olivier F, Wotherspoon SJ (2005) GIS-based application of resource selection functions to

19   the prediction of snow petrel distribution and abundance in East Antarctica: Comparing

20   models at multiple scales. Ecological Modelling, 189, 105-129.

1   Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape

2   and biogeographical scale levels in research and conservation. Biological Conservation, 117,

3   285-297.

4   Parmesan C, Ryrholm N, Stefanescu C et al (1999) Poleward shifts in geographical ranges of

5   butterfly species associated with regional warming. Nature, 399, 579-583.

6   Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across

7   natural systems. Nature, 421, 37-42.

8   Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on

9   terrestrial biota. Bulletin of the American Meteorological Society, 81, 443-450.

10 Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW (2010) Impacts of climate on

11 prey abundance account for fluctuations in a population of a northern wader at the southern

12 edge of its range. Global Change Biology, 16, 12–23.

13 Pearman PB, Randin CF, Broennimann O et al. (2008) Prediction of plant species

14 distributions across six millennia. Ecology Letters, 11, 357–369.

15 Pearson RG, Dawson TP, Berry PM, Harrison PA (2002) SPECIES A spatial evaluation of

16 climate impact on the envelope of species. Ecological Modelling, 154, 289-300.

17 Peterson AT (2003) Projected climate change effects on Rocky Mountain and Great Plains

18 birds: generalities of biodiversity consequences. Global Change Biology, 9, 647-655.

19 Peterson AT, Sánchez-Cordero V, Soberón J, Bartley J, Buddemeier RW, Navarro-Sigüenza

20 AG (2001) Effects of global climate change on geographic distributions of Mexican cracidae.

21 Ecological Modelling, 144, 21-30.

1   Phillips LB, Hansen AJ, Flather CH, Robison-Cox J (2010) Applying species-energy theory

2   to conservation: a case study for North American birds. Ecological Applications, 20, 2007-

3   2023.

4   Porporato A, Daly E, Rodriguez-Iturbe I (2004) Soil water balance and ecosystem response to

5   Climate Change. The American Naturalist, 164, 625-632.

6   R Development Core Team (2010) R: A language and environment for statistical computing.

7   R Foundation for Statistical Computing, Vienna, Austria.

8   Radford JQ, Bennett AF (2007) The relative importance of landscape properties for woodland

9   birds in agricultural environments. Journal of Applied Ecology, 44, 737–747.

10 Randin CF, Engler R, Normand S et al. (2009) Climate change and plant distribution: local

11 models predict high-elevation persistence. Global Change Biology, 15, 1557–1569.

12 Rapacciuolo G, Roy DB, Gillings S, Fox R, Walker K, Purvis A (2013) Climatic associations

13 of British species distributions show good transferability in time but low predictive accuracy

14 for range change. PLoS ONE, 7, e40212.

15 Renwick AR, Massimino D, Newson SE, Chamberlain DE, Pearce-Higgins JW, Johnston A

16 (2012) Modelling changes in species' abundance in response to projected climate change.

17 Diversity and Distributions, 18, 121-132.

18 Robbins CS, Bystrak D, Geissler P (1986) The Breeding Bird Survey: its first 15 years, 1965-

19 1979. USDI Fish and Wildlife Service Research Publication 157.

20 Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North

21 American birds that migrate to the neotropics. Proceedings of the National Academy of

22 Sciences USA, 86, 7658-7662.

1   Robinson RA, Baillie SR, Crick HQP (2007) Weather-dependent survival: implications of

2   climate change for passerine population processes. Ibis, 149, 357–364.

3   Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of

4   global warming on wild animals and plants. Nature, 421, 57-60.

5   Root TL, Schneider SH (1993) Can large-scale climatic models be linked with multiscale

6   ecological studies? Conservation Biology, 7, 256-270.

7   Rubidge EM, Patton JL, Lim M, Burton AC, Brashares JS, Moritz C (2012) Climate-induced

8   range contraction drives genetic erosion in an alpine mammal. Nature Climate Change, 2,

9   285-288.

10   Sauer JR, Hines JE, Fallon J, Pardieck KL, Ziolkowski DJ, Link WA (2011) The North

11   American Breeding Bird Survey, results and analysis 1966–2009. Version 3.23. US

12   Geological Survey Patuxent Wildlife Research Center. Laurel, Maryland.

13   Shirley SM, Yang Z, Hutchinson RA, Alexander JD, McGarigal K, Betts MG (2013) Species

14   distribution modelling for the people: unclassified landsat TM imagery predicts bird

15   occurrence at fine resolutions. Diversity and Distributions, 19, 855-866.

16   Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate change on the

17   population dynamics of a migratory songbird. Science, 288, 2040-2042.

18   Smith SE, Gregory RD, Anderson BJ, Thomas CD (2013) The past, present and potential

19   future distributions of cold-adapted bird species. Diversity and Distributions, 19, 352-362.

20   Stralberg D, Jongsomjit D, Howell CA, Snyder MA, Alexander JD, Wiens JA, Root TL.

21   (2009) Re-shuffling of species with climate disruption: A no-analog future for California

22   birds? PLoS ONE, 4, e6825.

1 Şekercioğlu ÇH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines.

2 Proceedings of the National Academy of Sciences USA, 101, 18042-18047.

3 Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature, 399, 213.

4 Thomas CD, Cameron A, Green RE et al. (2004) Extinction risk from climate change. Nature,

5 427, 145-148.

6 Thuiller W (2003) BIOMOD – optimizing predictions of species distributions and projecting

7 potential future shifts under global change. Global Change Biology, 9, 1353–1362.

8 Thuiller, W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental

9 range of data to project current and future species distributions. Ecography, 27, 165-172.

10 Tingley MW, Koo MS, Moritz C, Rush AC, Beissinger SR (2012) The push and pull of

11 climate change causes heterogeneous shifts in avian elevational ranges. Global Change

12 Biology, 18, 3279-3290.

13 Tittler R, Fahrig L, Villard MA (2006) Evidence of large-scale source-sink dynamics and

14 long-distance dispersal among Wood Thrush populations. Ecology, 87, 3029-3036.

15 Verburg PH, Neumann K, Nol L (2011) Challenges in using land use and land cover data for

16 global change studies. Global Change Biology, 17, 974–989.

17 Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's

18 Ecosystems. Science, 5325, 494-499.

19 Walther GR, Post E, Convey P et al. (2002) Ecological responses to recent climate change.

20 Nature, 416, 389-395.

1   Watling JI, Bucklin DN, Speroterra C, Brandt LA, Mazzotti FJ, Romañach SS (2013)

2   Validating predictions from climate envelope models. PLoS ONE, 8, e63600.

3   Welsh AH, Lindenmayer DB, Donnelly CF (2013) Fitting and Interpreting Occupancy

4   Models. PLoS ONE, 8,,e52015. doi:10.1371/journal.pone.0052015.

5   Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC (2008) Phylogenetic

6   patterns of species loss in Thoreau's woods are driven by climate change. Proceedings of the

7   National Academy of Sciences USA, 105, 17029-17033.

8   Wilson RJ, Gutiérrez D, Gutiérrez Illán J, Martínez D, Agudo R, Monserrat VJ (2005).

9   Changes to the elevational limits and extent of species' ranges associated with climate

10   change. Ecology Letters, 8, 1138-1146.

11   Wilson RJ, Gutiérrez D, Gutiérrez Illán J. & Monserrat VJ (2007) An elevational shift in

12   butterfly species richness and composition accompanying recent climate change. Global

13   Change Biology, 13, 1873-1887.

1 **Table 1.** List of climate variables included in the analyses. Values are given at route level in

2 each period as they were included in the analyses. Averages values are shown for all study

3 sites in the selected period and values in brackets show the ranges of the given variable in the

4 study system

Climate variable	Units	Mean [min-max]	
		1970-74	1998-02
June Maximum Temperature	℃	24.7 [13.0 – 39.9]	22.7 [11.0 – 39.1]
June Minimum Temperature	℃	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	℃	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	℃	-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]

5

6

1   **Figure legends**

2   **Fig 1**. Panel a: Map of the study area, showing the topographical heterogeneity of the five US

3   states (California, Idaho, Nevada, Oregon, Washington) and Canadian province of British

4   Columbia included. Panel b: Change (70-74 to 98-02) in average minimum temperature of the

5   coldest month (January). ΔTp varies from a cooling of > -1ºC (dark blue) to warming of > 5ºC

6   (dark red). Panel c): Change in average precipitation of the driest month (July), from a drying

7   of > -10 mm (dark brown) to increased precipitation of > 10 mm (dark blue). Panel d: Change

8   in average precipitation of the wettest month (December), from a drying of > -10 mm (dark

9   brown) to to increased precipitation of > 10 mm (dark blue). BBS routes used in the study are

10   shown in black in all maps.

11   **Fig 2.** Flow chart summarizing the model building and evaluation process.

12   **Fig 3.** Summary of model performance evaluation for a) distribution (presence/absence) and

13   b) abundance models. Presence/absence models were evaluated via AUC and abundance

14   models were evaluated using Spearman´s rank correlation coefficients between observed and

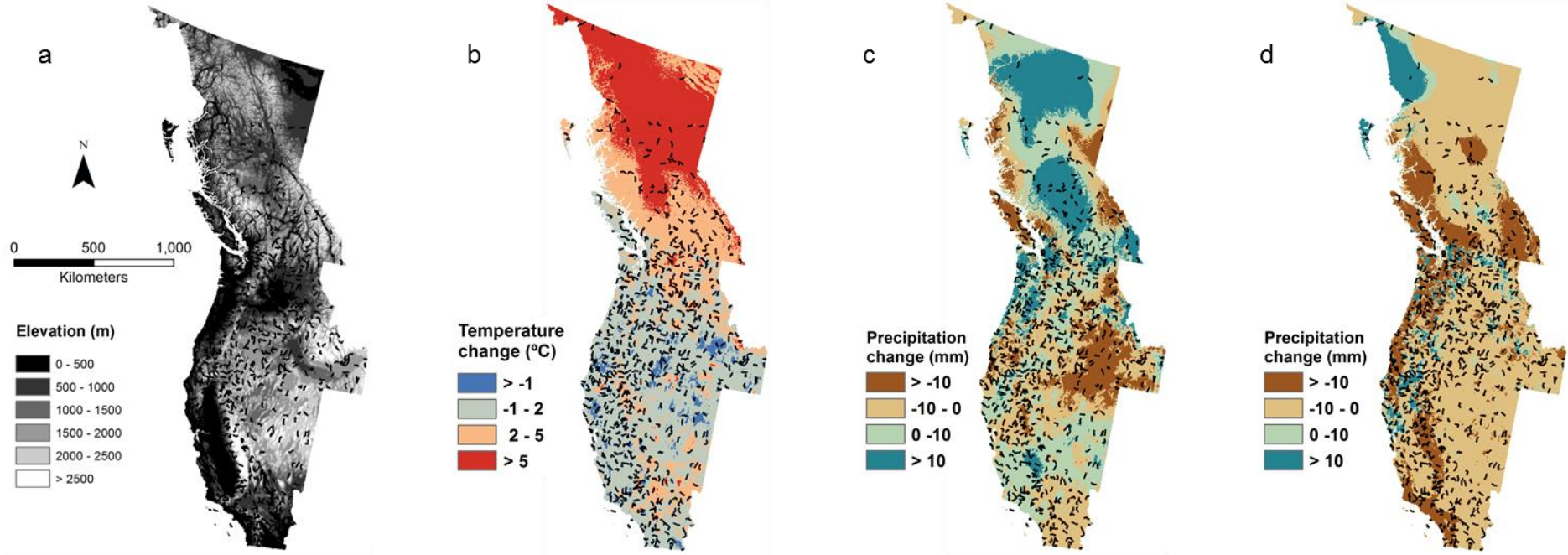15   predicted abundance of each target species at each route.

16   **Fig 4.** Plot of mean change in suitability of colonized versus extinct routes for the target

17   species (each species is represented by a black dot). The dashed line shows no explanation

18   ability (same change in suitability for colonized and extinct routes). Local

19   colonization/extinction of the species located above the line (ideally in the top-left quadrant of

20   the plot) are predicted by the occupancy models through time.

21   **Fig 5** Plots of observed and predicted abundance changes for two exemplar species,

22   Loggerhead shrike (*Lanius ludovicianus*) (Left), and Purple finch (*Haemorhous purpureus*)

23   (Right). Scatter plots show evaluation of the abundance models through time (Loggerhead

1 skrike, Spearman´s ρ of 0.64 , based on 72 routes; Purple finch, Spearman´s ρ of 0.33 , based

2 on 110 routes). Maps show locations of observed (a panels) and predicted (b panels)
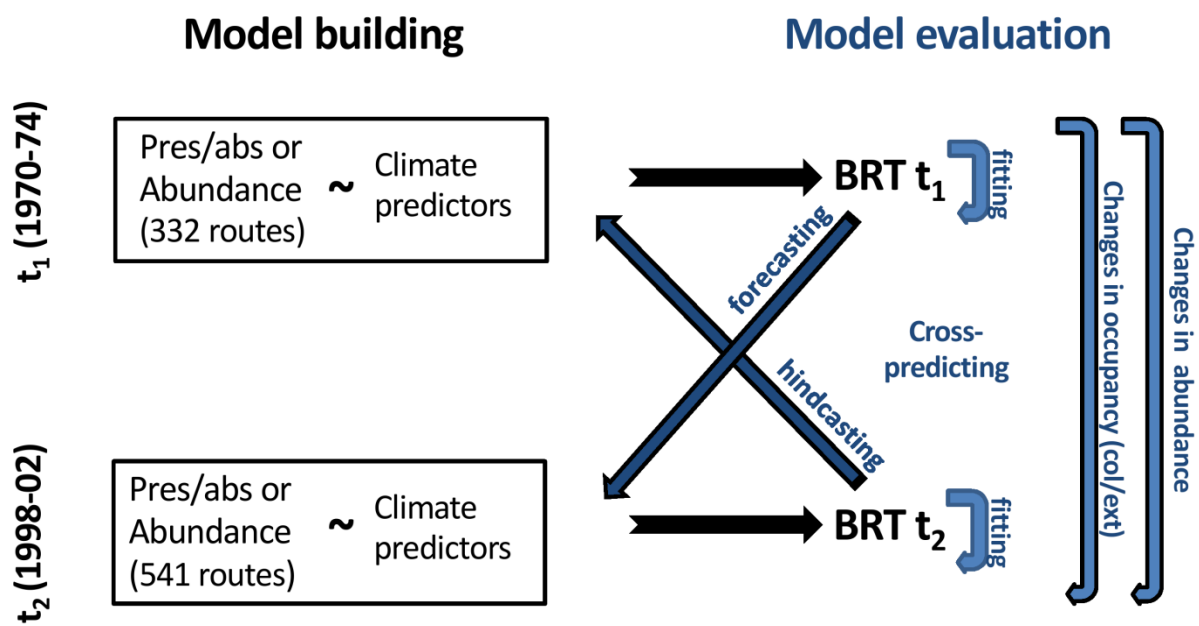
3 abundance changes.

4 **Fig 6** (a) Relative contribution of the climate factors included in the models. Plot shows

5 results obtained in presence/absence models (left panel) and abundance models (right panel).

6 Black bars show the percentages (x axes) of models where a given climate variable was

7 ranked as the most important according to its relative contribution. Grey bars show the

8 percentages of models where a given variable was ranked as one of the top three most

9 important variables. Results are shown for the forecasting evaluation only. Fig 6b shows the

10 same results, but only for the target species that obtained an evaluation performance

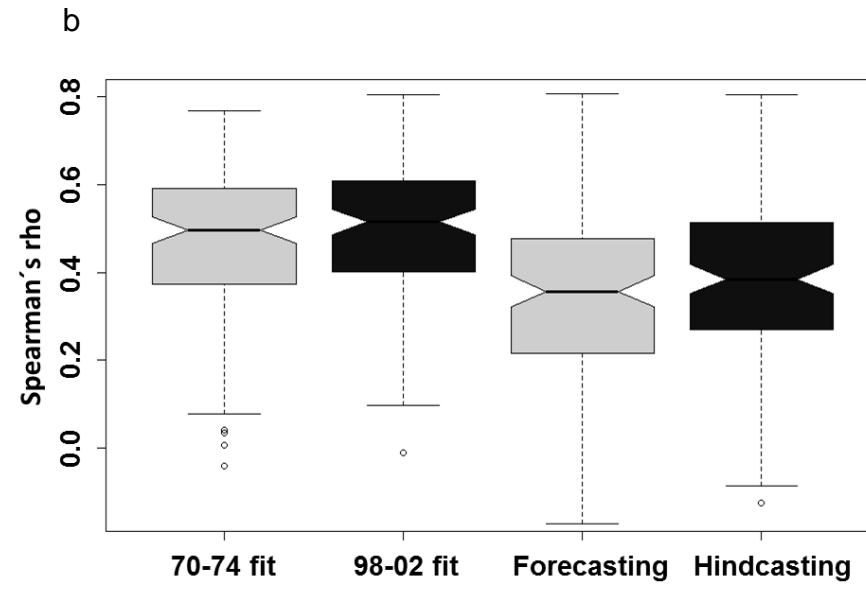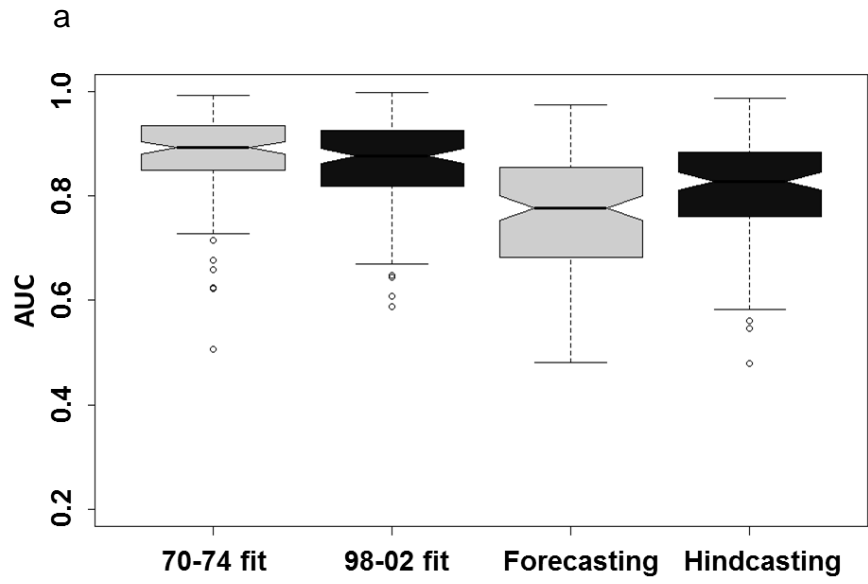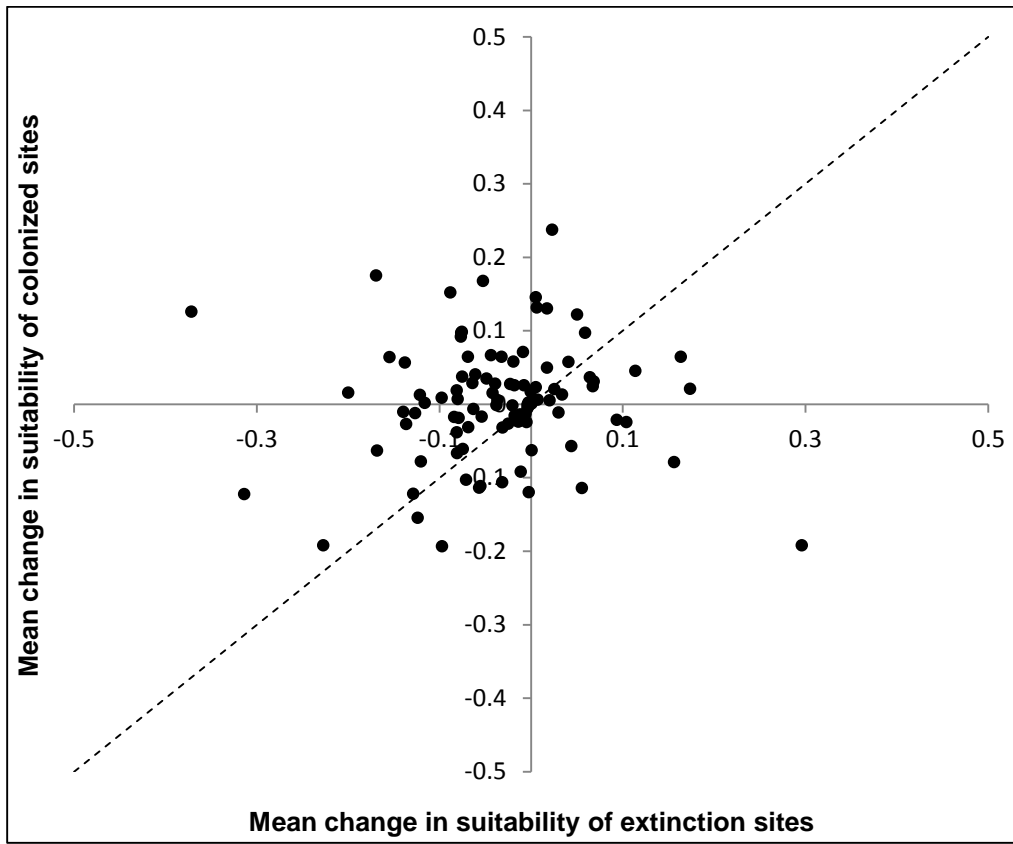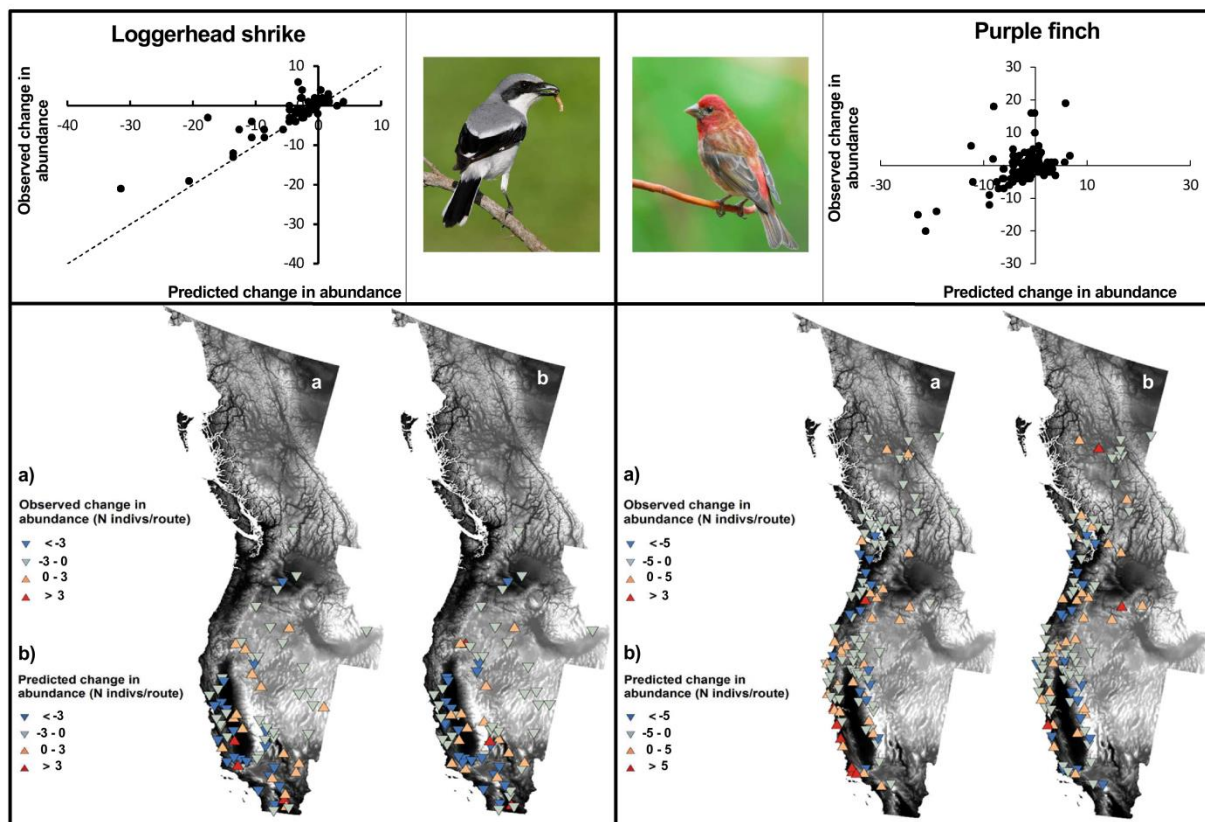11 (Spearman´s ρ) above 0.4 (34 species).

1   Fig 1

2

1   Fig 2

2

1   Fig 3

a

b

1   Fig 4

Mean change in suitability of colonized sites

Mean change in suitability of extinction sites

2

1   Fig 5

2

1   Fig 6

2   a

7   b

8