

Population trends influence species ability to track climate change

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Abstract

Shifts of distributions have been attributed to species tracking their fundamental climate niches through space. However, several studies have now demonstrated that niche tracking is imperfect, that species' climate niches may vary with population trends, and that geographic distributions may lag behind rapid climate change. These reports of imperfect niche tracking imply shifts in species' realized climate niches. We argue that quantifying climate niche shifts and analyzing them for a suite of species reveal general patterns of niche shifts and the factors affecting species' ability to track climate change. We analyzed changes in realized climate niche between 1984 and 2012 for 46 species of North American birds in relation to population trends in an effort to determine whether species differ in the ability to track climate change and whether differences in niche tracking are related to population trends. We found that increasingly abundant species tended to show greater levels of niche expansion (climate space occupied in 2012 but not in 1980) compared to declining species. Declining species had significantly greater niche unfilling (climate space occupied in 1980 but not in 2012) compared to increasing species due to an inability to colonize new sites beyond their range peripheries after climate had changed at sites of occurrence. Increasing species, conversely, were better able to colonize new sites and therefore showed very little niche unfilling. Our results indicate that species with increasing trends are better able to geographically track climate change compared to declining species, which exhibited lags relative to changes in climate. These findings have important implications for understanding past changes in distribution, as well as modeling dynamic species distributions in the face of climate change.

Keywords: birds, Breeding Bird Survey, change-point analysis, climate niche, Grinnellian niche

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Introduction

Of the many ways in which climate change impacts wildlife, geographic range shifts have perhaps received the most attention. The influence of climate change on shifting species distributions appears to be nearly universal, with empirical examples spanning a wide range of taxa (Smith, 1994; Pauli *et al.*, 1996; Hickling *et al.*, 2005, 2006; Perry *et al.*, 2005; Foden *et al.*, 2007; Hitch & Leberg, 2007; Moritz *et al.*, 2008; Jones *et al.*, 2010; Last *et al.*, 2011; Yamano *et al.*, 2011). Although exceptions exist, the predominant pattern is that in recent decades of warming temperatures, species have shifted their distributions poleward and up in elevation (Parmesan *et al.*, 1999; Walther *et al.*, 2002; Hickling *et al.*, 2006; La Sorte & Thompson, 2007; Moritz *et al.*, 2008; Chen *et al.*, 2011; Auer & King, 2014; Bateman *et al.*, 2016). The proposed mechanism for these climate driven range shifts is that species are geographically tracking their climate

niche (Devictor *et al.*, 2008; Tingley *et al.*, 2009; La Sorte & Jetz, 2012; Tayleur *et al.*, 2015). According to the niche tracking concept, as climates change, a species will vacate sites that are no longer climatically suitable and colonize new sites that now fall within its climate niche, such that the range of climate conditions occupied by the species is maintained. If species are able to track their climate niche through time in this way, current species–climate associations can be used to predict future species distributions under various climate change scenarios (Pearson & Dawson, 2003; Hijmans & Graham, 2006). This correlative modeling approach has become an important tool in understanding biotic responses to climate change (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Colwell *et al.*, 2008; Ralston & Kirchner, 2013), and for prioritizing conservation and management decisions that incorporate climate change (Schuetz *et al.*, 2015; Sutton *et al.*, 2015).

Importantly, both the niche tracking concept and its application in predictive species distribution modeling assume niche conservatism (Soberón, 2007; Soberón & Nakamura, 2009). That is, they assume that in the

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future, a species will occupy the same climate conditions that it occupies today. Several studies have supported niche conservatism on both ecological and evolutionary timescales (Peterson *et al.*, 1999; Wiens & Graham, 2005; Peterson, 2011). However, these studies primarily focused on conservation of the *fundamental* niche (Hutchinson, 1957), for example, species' inherent climate tolerances. A separate question is whether the *realized* climate niche, or the range of conditions actually occupied by a species, is also conserved, which assumes the absence of any lags or limitations to dispersal. Several studies have demonstrated that, in reality, species are likely lagging behind rapid climate change (Menéndez *et al.*, 2006; Foden *et al.*, 2007; Devictor *et al.*, 2008; Bertrand *et al.*, 2011; La Sorte & Jetz, 2012). Therefore, in the absence of perfect tracking and given rapid environmental change, we may expect changes in species' realized climate niches (Sutton *et al.*, 2015). Understanding how realized niches change with climatic conditions will allow us to better understand recent range shifts in response to climate change, as well as the growing number of examples in which species' ranges have shifted in a manner contrary to predictions from theory (Tingley *et al.*, 2012; Foster & D'Amato, 2015; Tayleur *et al.*, 2015).

In a recent study, we demonstrated population trends in the last 33 years significantly and directly influenced realized climate niche breadth for a group of 46 North American breeding bird species (Ralston *et al.*, 2016). That realized climate niches have changed is consistent with the hypothesis that species distributions are lagging behind rapid environmental change on a short timescale (Devictor *et al.*, 2008; La Sorte & Jetz, 2012; Sutton *et al.*, 2015). However, because changes in climate niche breadth were significantly and positively correlated with trends in abundance and with changes in distributional extent (Ralston *et al.*, 2016), an alternative hypothesis is that changes in niche breadth might be explained by demographic and geographic expansion or contractions independent of climate change. Therefore, it remains unclear whether changes in realized climate niche on the ecological time scale are the result of differential demographic and geographic expansion, differences in species' capacity to track climate change, or some combination of these factors. For example, observed increases in climate niche breadth for species with increasing trends may be the result of geographic expansion into new conditions, or alternatively, persistence at sites where conditions are changing. Conversely, decreases in realized climate niche breadth for declining species might be the result of range contractions or an inability to track historical niche conditions to new sites. While these alternative hypotheses are not mutually exclusive, and both could

lead to positive correlations between abundance, climate niche breadth, and distributional extent, disentangling the relative contribution of each to changes in climate niche breadth will increase our understanding of species' responses to climate change. Here, we aim to differentiate between the effects of geographic expansion and *in situ* climate change on changes in realized climate niche in North American breeding birds. By doing so, we illustrate how species differ in the ability to track climate change and determine whether that ability is related to population trends.

Materials and methods

Population trends and occurrence data

We obtained estimates of trends in abundance for breeding birds from the publicly available North American Breeding Bird Survey (BBS) for 1980–2012 (Link & Sauer, 2002; Sauer *et al.*, 2014; <http://www.mbr-pwrc.usgs.gov/bbs/>). When estimating trends, BBS scientists fit hierarchical models to account for observer effects and covariates that might influence detection (Link & Sauer, 2002; Sauer & Link, 2011). We downloaded trend estimates for a set of 46 species, which represented species with the highest BBS credibility measure, distributions that were at least 70% covered by the BBS, and a minimum of 600 occurrences in both 1980 and 2012. These conditions ensured that we had high-quality data and that we were able to capture the majority of each species' climate niche. This was an ecologically and taxonomically diverse suite of species that differed in terms of habitat use, nesting, and foraging guilds, and included species from 21 different avian families (Supporting information). Our dataset included 23 species with significantly declining trends (negative trend and 95% CI not overlapping with 0.00), 12 species with significantly increasing trends (positive trend and 95% CI not overlapping with 0.00), and 11 species with stable trends (95% CI that overlap with 0.00) for the time period between 1980 and 2012.

Quantifying shifts in realized climate niche

We calculated climate niche shifts through a three stage process. First, we calculated the climatic space (see below) of the entirety of the BBS survey area by using all BBS survey routes surveyed in both 1980 and 2012 as input data, hereafter 'surveyed climate space'. Second, we calculated the realized climate niche of each species by calculating the proportion of the surveyed climatic space actually occupied by each species, in each time period, hereafter 'occupied climate space'. Third, we quantified climate niche shift for each species by comparing the overlap of occupied climate space between 1980 and 2012. (Broennimann *et al.*, 2012; Petitpierre *et al.*, 2012; Guisan *et al.*, 2014). To control for the influence of annual fluctuations in species occurrence or detection, we calculated realized niches from a 5-year window of occurrences for each time period. The '1980' realized climate niches were calculated using

BBS occurrences from 1980 through 1984, and the '2012' niches were calculated using BBS occurrence data from 2008 through 2012. We used a principal components analysis (PCA) to convert a geographic map of BBS occurrences into an environmental space with two axes, one defined by temperature (PCtemp) and the other by precipitation (PCprec). PCtemp was the first axis of a PCA on four bioclimatic temperature variables: annual mean temperature, temperature seasonality (standard deviation * 100), maximum temperature of warmest month, and minimum temperature of coldest month. PCprec was the first axis of a PCA on four bioclimatic precipitation variables: annual precipitation, precipitation seasonality (coefficient of variation), precipitation of wettest quarter, and precipitation of driest quarter. We chose these bioclimatic variables as they describe the means, extremes, and seasonality of temperature and precipitation, and because they have been successfully combined with BBS data in previous studies that examine bird responses to climate change (e.g., Bateman *et al.*, 2016). We calculated all bioclimatic variables in the R package *dismo* (Hijmans *et al.*, 2014) from Climate Research Unit monthly climate data at a 0.5-degree resolution (Harris *et al.*, 2014). The PCAs used to calculate PCtemp and PCprec were calibrated using climate data from all BBS routes surveyed in 1980–1984 and 2008–2012 combined. PCtemp explained 77.99% of the variation in bioclimatic temperature variables, and PCprec explained 74.48% of the variation in bioclimatic precipitation variables in these two time periods combined. PCtemp and PCprec loaded positively with bioclimatic variables describing minimum, maximum, and mean temperature and precipitation, respectively. This means larger PCtemp values represent warmer conditions, while larger PCprec values represent wetter conditions.

We divided the climate space defined by minimum and maximum PCtemp and PCprec values into a grid of 100 × 100 cells (hereafter 'climate grid cells'). We calculated the density of occurrences for each species in each climate grid cell simply as the number of BBS occurrences that correspond to that climate grid cell. We then applied a kernel density function (Worton, 1989) to determine the smoothed density of each species occurrences in every climate grid cell (Broennimann *et al.*, 2012). Any cell with a smoothed density value greater than zero can be interpreted as occupied by the species in that time period. We therefore estimated the climate niche for each species in 1980 and 2012 as the range of climate conditions occupied in that time period (i.e., the collection of grid cells with smoothed densities greater than zero, hereafter, 'occupied climate grid cells'). We note that by including only climate variables in our analyses, we are estimating only the realized *climate* niche for each species and acknowledge that other abiotic and biotic factors may also be important to a species niche and to delimiting distributions. For each species, we then overlapped the 1980 and 2012 estimated climate niches in gridded climate space to calculate two niche shift metrics: niche expansion and niche unfilling (Petitpierre *et al.*, 2012; Guisan *et al.*, 2014; Fig. 1). Niche expansion represents newly occupied climate niche space not historically occupied and is calculated as the proportion of climate grid cells occupied in 2012 that were not occupied in 1980. Niche unfilling

represents historical climate niche conditions no longer being occupied and is defined as the proportion of climate grid cells occupied in 1980 that were not occupied in 2012. Importantly, we considered only climate space surveyed in both time periods, meaning niche shift is not an artifact of differences in the climate surveyed, but indicative of real changes in species' climate niche occupancy. Each niche shift metric was measured only within the 75th percentile of surveyed climate space (Petitpierre *et al.*, 2012; Fig. 1). The 75th percentile was used to remove marginal conditions at the peripheries of surveyed climate space (Petitpierre *et al.*, 2012); however, delimiting the marginal habitats with different percentiles (75th, 90th, 100th) did not qualitatively influence our results. We used linear regressions to examine the relationship between population trend and each niche shift metric.

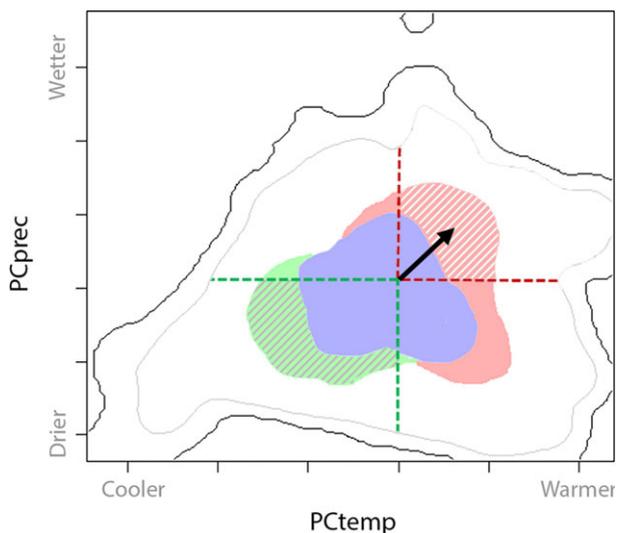


Fig. 1 An example climate niche diagram demonstrating niche shift metrics and climate response. Niche shift metrics were calculated within climate space surveyed by BBS routes in both 1980 and 2012 time periods (black outline) and analyzed only within 75th percentile of surveyed climate space (gray outline). Niche stability (blue shading) is defined as the climate conditions occupied by a species in both 1980 and 2012; niche unfilling (green shading) is the proportion of the 1980 niche not occupied by the species in 2012; and niche expansion (red shading) is the proportion of the 2012 niche not occupied by the species in 1980. For each species, we measure the direction of climate change (black arrow) relative to the median conditions at sites of 1980 occurrences (origin of black arrow), and defined all climate space in the same direction as the Climate Change Quadrant (CCQ; red dashed lines), and all climate space in the opposite direction as the Climate Change Opposite Quadrant (CCOQ; green dashed lines). We compared the amount of expansion in the CCQ (red shading with hash lines), and the amount of unfilling in the CCOQ (green shading with hash lines) to the relative amount of climate space in each of these quadrants to calculate the Climate Expansion Index and the Lagging Index, respectively.

To ensure the relationships we observe between trend and niche shift metrics were not artifacts of changes in prevalence (number of occurrences), we recalculated niche expansion and unfilling while controlling for the increasing prevalence that occurred between 1980 and 2012 for all species. We took 100 random subsamples of the 2012 occurrence data of equal size to the number of 1980 occurrences for that species. We then estimated the 2012 niche for each random subsample and calculated niche shift metrics for each by comparing them to the estimated 1980 niche. Observed patterns between mean niche expansion and unfilling from these 100 subsets were all nearly identical to those calculated when using all of the 2012 occurrences (Appendix S1). We therefore only report results from analyses using all occurrences.

Quantifying niche tracking and lagging

Niche expansion could result from a species geographically moving into new conditions or from a species continuing to occupy sites where conditions have changed. To distinguish between these two alternative processes, we developed the Expansion Index (EI). To calculate each species' EI, we first determined how climate has changed at sites where the species occurred in 1980. To do this, we calculated the change in the median PCtemp and PCprec between 1980 and 2012 for BBS sites occupied in 1980. A positive change in median PCtemp indicated BBS sites occupied in 1980 have generally warmed, while a positive change in median PCprec indicated sites occupied in 1980 have gotten wetter (Fig. 1). We then considered all climate grid cells in the same direction as climate change to be within the Climate Change Quadrant (CCQ). In other words, if 1980 occurrence sites have gotten warmer and wetter, all climate grid cells warmer and wetter than the median values for 1980 occurrences would be considered in the CCQ (Fig. 1). We calculated EI for each species using the equation $EI = (E_{ccq} - \zeta_{ccq}) / (1 - \zeta_{ccq})$, where E_{ccq} is the proportion of niche expansion (newly occupied climate grid cells) that falls within the CCQ, and ζ_{ccq} is the proportion of all surveyed climate space that falls within the CCQ (Fig. 1). By focusing on niche changes in the CCQ, we used EI to approximate geographic changes at the trailing edge of a range shift, for example, at the southern periphery of a warming range. Our null expectation, if climate niche is expanding randomly or equally on all niche peripheries, is that E_{ccq} would equal ζ_{ccq} . This would result in an EI value of 0. EI values close to zero therefore support the hypothesis that niche expansion is the result of geographic expansion, independent of climate change. Alternatively, positive EI values indicate that the climate niche is not expanding on all peripheries, but specifically into conditions consistent with changing climate. We assumed that birds with positive EI were not actively colonizing sites at the extreme of their climatic niche but, instead, persisting and experiencing newly extreme (i.e., warmer) climates. The maximum value of EI is 1, indicating that all niche expansion can be explained by a species occupying the same sites in 1980 and 2012, and climate changing at those sites. Therefore, positive EI values close to 1 would support the hypothesis that niche expansion is explained by climate

change at historical sites of occurrence. A negative EI value indicates that a larger than expected proportion of niche expansion falls outside of the CCQ. This could result either from widespread expansion into new conditions on all niche peripheries, or alternatively from lower tolerance of changing conditions resulting in greater extinction within the CCQ. To test between these alternatives, we compared EI to the relative amount of niche expansion and extinction within the CCQ. Extinction in the CCQ was calculated as the proportion of BBS sites in the CCQ occupied in 1980 that were no longer occupied in 2012. BBS sites with 2012 conditions warmer and wetter than each species' median 1980 PCtemp and PCprec were considered in the CCQ.

Just as niche expansion can arise through different geographic processes, niche unfilling could result from extinctions within a species' range or from a species failing to colonize new sites as its climate niche is shifted in space by climate change. To measure the relative influence of climate change on the observed niche unfilling for each species, we developed the Lagging Index (LI). We used LI to determine how well a species tracked its climate niche through space to new locations, or alternatively lagged behind climate change. To calculate LI, we first found the 'Climate Change Opposite Quadrant' (CCOQ) for each species, defined as all climate grid cells in the opposite direction of climate change at 1980 occurrences (Fig. 1). For example, if the 1980 occurrence sites for a species have become warmer and wetter, all climate grid cells cooler and drier than the median PCtemp and PCprec values of 1980 occurrences would be considered in the CCOQ (Fig. 1). We then calculated LI using the equation $LI = (U_{ccoq} - \zeta_{ccoq}) / (1 - \zeta_{ccoq})$, where U_{ccoq} is the proportion of niche unfilling (newly unoccupied climate grid cells) that falls within the CCOQ, and ζ_{ccoq} is the proportion of all surveyed climate space that falls within the CCOQ (Fig. 1). Our null expectation, if a niche is unfilling randomly or equally on all niche peripheries, is that U_{ccoq} would equal ζ_{ccoq} , resulting in a LI value of 0. A positive LI value indicates lagging and means that a larger proportion of niche unfilling occurred within the CCOQ, and is because individuals failed to colonize new sites, especially at the leading edge of the range shift. By focusing on niche changes in the CCOQ, LI approximates geographic changes at the leading edge of a range shift, for example, the northern periphery of a warming range. A negative LI value means that a smaller than expected proportion of niche unfilling fell within the CCOQ. A negative LI value indicates niche tracking. For example, if sites of 1980 occurrence have gotten warmer and wetter, but a species showed very little unfilling of cool and dry climate space, we can conclude that the species has been able to colonize new sites to maintain those niche conditions.

To build support for our geographic interpretation of LI, we also quantified the colonization of BBS sites inside and outside CCOQ for each species. BBS sites with 2012 conditions cooler and drier than median 1980 PCtemp and PCprec for the each species' occurrences were considered in the CCOQ for that species. Colonization was measured as the proportion of BBS routes occupied in 2012 that were not occupied in the 1980 time period. We interpreted a negative LI value as indicative

of niche tracking and therefore predicted species with low LI values to show higher colonization rates in the CCOQ compared to species with high LI values. Furthermore, we predicted species with low LI values to show higher colonization in the CCOQ compared to outside the CCOQ. Importantly, this would support the hypothesis that low unfilling in the CCOQ is truly the result of niche tracking, and not expansion on all niche peripheries.

Influences of trend on niche tracking

We used generalized additive models (GAMs) to fit relationships between population trends and EI and LI because the relationship between trend and the climate response indices were nonlinear. We then conducted change-point analyses (Killick & Eckerly, 2014) on the predicted GAM values to statistically identify trend thresholds corresponding to changes in the mean and variation of EI and LI (Cury *et al.*, 2012; Karr *et al.*, 2015). Change-point analyses were implemented in the R package *changepoint* (Killick & Eckerly, 2014). We estimated 95% confidence intervals around the trend thresholds using a bootstrap resampling approach in which the data were resampled with replacement 1000 times, and the threshold was calculated from each of the 1000 resampled datasets. The 2.5% and 97.5% quantiles of the 1000 threshold estimates were used as the threshold 95% confidence interval boundaries.

Finally, to build support for our interpretation of EI and LI, we explored an alternative method of comparing observed changes in niche metrics to those expected under a null model of complete geographic lagging. In this approach, we calculated niche expansion and unfilling for each species under a null model of lagging by forcing its 2012 occurrences to be identical to its 1980 occurrences. Results from this approach were consistent with our EI and LI results and so are only discussed further in the online supplemental materials (Appendix S2).

All of the above niche shift and statistical analyses were performed in the program R version 3.2.4 (R Core Team, 2016), and we provide scripts used to perform these analyses in the Supporting information.

Results

As we predicted, niche unfilling was significantly and negatively related to population trend ($\beta = -0.003$, $P = 0.001$, $R^2 = 0.221$), with declining species showing more niche unfilling than species with increasing trends. Also as predicted, niche expansion was significantly and positively related to population trend ($\beta = 0.003$, $P = 0.033$, $R^2 = 0.079$). Mean EI was not significantly different from zero when averaged across all species ($\mu = 0.013$, $t = 0.378$, $df = 45$, $P = 0.707$), meaning that across species there was general support for the hypothesis that niche expansion reflects geographic expansion. However, EI and the apparent influence of climate change on niche expansion varied greatly across species (range EI: -0.637 to 0.713 ; Appendix S3).

Twenty-five of the 46 species (54.3%) had a negative EI value, implying niche expansion independent of climate change (Fig. 2a). On the other hand, 21 of the 46 species (45.7%) had a positive EI value, supporting the hypothesis that niche expansion for these species was likely a result of climate change at occupied sites. Large positive EI values tended to be found in species showing overall declines and large amounts of niche expansion (Fig. 2b). For these species, most niche expansion was found in the CCQ and therefore likely the result of climate change at occupied sites. Despite this, we found little evidence that EI was influenced by population trend (Fig. 3a). While change-point analysis did identify a change in mean and variation of EI at a population trend of -1.83 , we were cautious in interpreting this threshold because the bootstrap-estimated confidence intervals around the threshold were rather large (-2.1 to 0.96), and mean EI above and below this threshold was not significantly different ($t = 0.794$, $df = 3.20$, $P = 0.482$). Although extinction in the CCQ was greater in declining species than in increasing species ($t = 2.551$, $df = 32.66$, $P = 0.016$), the low mean EI values indicate that extinctions generally did not occur disproportionately in the CCQ.

Mean LI was significantly greater than zero when averaged across all species ($\mu = 2.43$, $t = 3.923$, $df = 45$, $P < 0.001$), supporting the hypothesis that in general, niche unfilling was the result of lagging. However, LI also varied greatly across species (range: -0.661 to 1.00 ; Supporting information), with some (13/46, 28.2%) having little of their niche unfilling in the CCOQ. This result suggests that there is a limited influence of climate change on niche unfilling for these species, and they have been able to track their niche to new sites (e.g., Fig. 2c). Yet other species (31/46, 67.4%) showed a larger proportion of unfilling in the CCOQ, indicating lagging, or an inability to track climate change at the leading edge (e.g., Fig. 2d). The degree to which species were able to track climate change was largely influenced by population trend. Using change-point analysis, we found a threshold in the lagging response of species to climate change when population trends drop below -0.45 (95% CI: -0.57 to 0.56 ; Fig. 3b). Species with population trends above this threshold had significantly lower LI than species with declining trends below this threshold ($t = 2.589$, $df = 43.93$, $P = 0.013$), with many increasing species falling below a LI of zero. These results suggest that species with increasing trends have been better able to track their 1980 climate niche to new sites, whereas declining species were more likely to lag behind climate change. Analyses of colonization rates support our geographic interpretations of LI results. Colonization was greater inside the CCOQ for increasing species than it was for decreasing

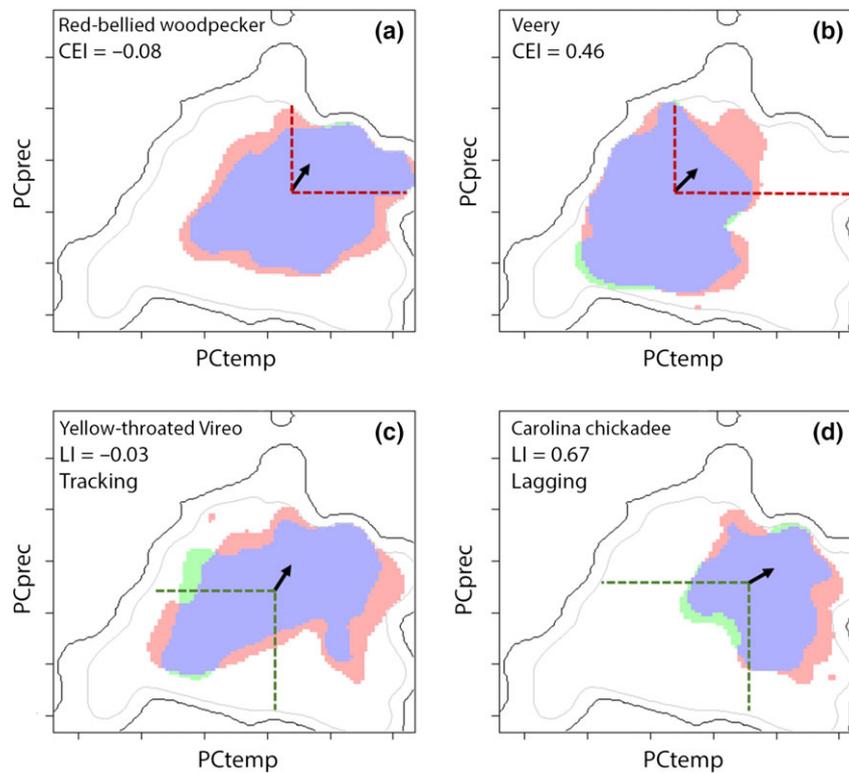


Fig. 2 Climate niche diagrams for four example species demonstrating the range of Expansion Index (EI) and Lagging Index (LI) values, and the relative influence of climate change (black arrow) on these climate response indices. (a) Species with low EI values tended to be geographically expanding with niche expansion (red shading) on all niche margins. (b) Species with high EI tended to be declining with niche expansion confined to the Climate Change Opposite Quadrant (CCOQ; red dashed line). (c) Species with low LI values showed very little niche unfilling (green shading) in the Climate Change Opposite Quadrant (CCOQ; green dashed line), indicating an ability to track their climate niche to new sites. (d) Species with high LI values had a larger proportion of unfilling falling within the CCOQ, indicating lagging. a and c represent species with relatively little influence of climate change on niche expansion and unfilling, respectively. b and d represent species with greater influence of climate change on niche expansion and unfilling, respectively. Climate niche diagrams for all 46 species of North American birds used in our analyses are included in the Appendix S3.

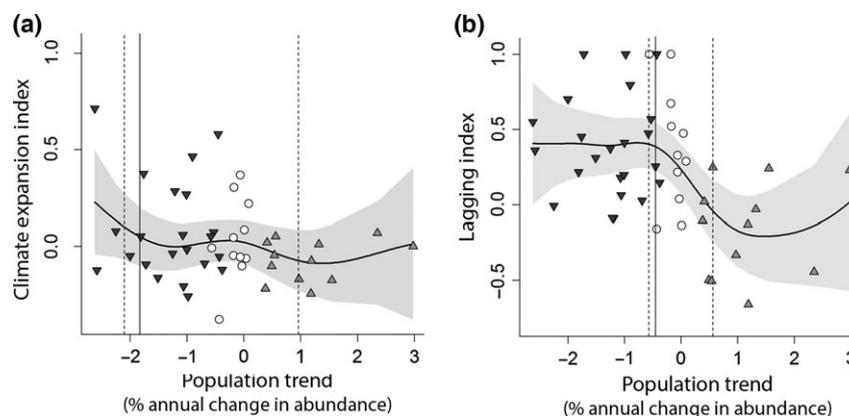


Fig. 3 Relationships between population trends and Climate Expansion Index (a) and Lagging Index (b) fit with generalized additive models (GAMs). Thick black lines are predicted values from GAMs and gray shading is the standard error associated with predicted values. Down-pointing dark gray triangles represent declining species, white circles represent species with stable trends, and up-pointing light gray triangles represent species with increasing trends. Vertical lines represent change-points (solid lines) at which the slopes of climate response indices statistically change, along with 95% confidence intervals (dashed lines).

species ($t = -3.56$, $df = 13.76$, $P = 0.003$), and, importantly colonization for increasing species was greater inside CCOQ than outside CCOQ, although this difference was not significant ($t = 1.85$, $df = 17.96$, $P = 0.081$). These results demonstrate that lack of niche unfilling for increasing species is due specifically to niche tracking at the leading edge and not simply range-wide geographic expansion.

Discussion

We present evidence that population trends influence species' ability to track climate change. Most species are exhibiting shifts in their realized niches in response to climate change as they either broaden the range of climate conditions they inhabit in the case of increasing species or lag behind climate change in the case of declining species. These results expand on our previous results (Ralston *et al.*, 2016) that showed climate niche breadth and population trends are positively correlated. We now demonstrate for the first time that decreasing climate niche breadth in declining species is the result of greater extinction rates at sites influenced by climate change and thus less niche expansion, as well as a failure to track historical niches beyond range peripheries and thus more niche unfilling. Conversely, increasing climate niche breadth in species with increasing trends results from greater niche expansion because of persistence at historical sites and geographic expansion beyond range peripheries; as well as a greater ability to track climate niches and thus very little niche unfilling.

Our results are consistent with previous studies on wintering birds in North America (La Sorte & Jetz, 2012) and breeding birds elsewhere (Devictor *et al.*, 2008) that demonstrate general patterns of geographic lagging. For example, Devictor *et al.* (2008) found that French birds are tracking climate change by shifting their ranges northward, but range shifts have not completely kept up with climate change, indicating some degree of lagging. Tingley *et al.* (2009) also found changes in realized climate niche within California bird species over the last century of climate change, but categorized those changes as niche tracking if they were changes toward a historical niche centroid. We take a different approach by quantifying the degree to which niche changes result from *in situ* climate change. We find that for most of our study species, at least some niche unfilling and niche expansion is the result of climate change, and therefore geographic lagging.

Quantifying tracking vs. lagging by using a continuous index (i.e., Lagging Index, LI) allowed us to examine differences in tracking ability across species. In doing so, we found a likely threshold response in

population trend and species' geographic responses to climate change. Declining species lagged to a greater degree behind climate at the leading edge of range shifts while increasing species were better at tracking their niche to new sites (Fig. 3b). The observed threshold (trend = -0.54) is close to our greatest observed significantly negative trend (Northern Mockingbird, trend = -0.38). This suggests that as trends become negative there is a real shift in the ability to track climate change, perhaps due to decreased availability of dispersers. Metapopulation theory posits that large or increasing populations (i.e., 'sources') will produce more dispersers than small or declining populations (i.e., 'sinks') and thus colonize new sites at a higher rate (Pulliam, 1988; Hill *et al.*, 1996; Hanski *et al.*, 2000). Our results support that these metapopulation dynamics may be important in species' geographic responses to climate change. Future work focused on relating metapopulation dynamics and population processes to range shifts may be especially important in understanding biotic responses to climate change (Keith *et al.*, 2008; Anderson *et al.*, 2009).

We separately examine niche expansion in the direction of climate change and niche unfilling in the opposite direction of climate change to disentangle how species have responded at the trailing edge (i.e., within their historical distribution) and leading edge (i.e., beyond their historical distribution) of range shifts, respectively. We found important differences in how climate change is influencing species at these margins. Specifically, we found that declining species tended to be more affected by climate change at the trailing edge while being unable to track their climate niche at the leading edge. This may result in any distributional shifts observed in declining species occurring primarily because of effects at the trailing edge, while the leading edge may shift very little in these species. Conversely, any distributional shifts in increasing species may be occurring primarily at the leading edge, as these species are better able to track to new locations, and very little movement of the trailing edge, as these species are better able to deal with changing conditions. It is important to clarify that here, we use 'tracking' at the 'leading edge' not necessarily to mean northward movement, but the movement of a species to any newly suitable site not previously occupied. We also acknowledge that our analyses are to some extent constrained by the availability of occurrence data beyond current range peripheries, especially for species with range boundaries outside of the BBS survey area.

Previous studies that examined whether species' ranges are shifting at the same pace as climate or whether mean occupied climate space has shifted may confound species' responses at the leading and trailing

edges (Devictor *et al.*, 2008; Tingley *et al.*, 2009; La Sorte & Jetz, 2012). To effectively conserve species, it will be important to understand these two potentially separate responses to climate change. Conservation and management approaches to climate change vary widely (Heller & Zavaleta, 2009), but generally focuses on either one range margin or the other. For example, some conservation strategies focus on promoting species' ability to track climate change by creating poleward-oriented dispersal corridors (Halpin, 1997) or by directly assisting in poleward migrations (McLachlan *et al.*, 2007). Others focus on conservation at the trailing edge by protecting current habitats, promoting climate change resilience (Morecroft *et al.*, 2012), or identifying potential refugia where conditions will remain suitable (Keppel *et al.*, 2012). While the trailing edge of species' ranges may hold valuable diversity (Hampe & Petit, 2005), it seems that the rapid pace and inevitability of climate change will make promoting the ability to track climate niches through space increasingly important for conservation. However, for declining species unable to naturally track climates northward, promoting persistence in currently occupied habitats and identifying climate refugia not requiring dispersal may be the most beneficial. The species-level information on niche tracking provided by our methods may be useful for assessing the appropriateness of alternative conservation actions.

It is difficult to determine the direction of causality in the correlation between population trends and niche tracking/lagging. Species with increasing trends may produce greater numbers of dispersers and therefore be more likely to colonize newly suitable areas. Alternatively, greater ability to disperse and track climate change may have promoted greater increases in abundance for these species. Many of the lowest LI values (i.e., the best trackers) are for species known to be demographically or geographically expanding over the study period. These include species of the historically 'Carolinian avifauna', such as Red-bellied Woodpecker (*Melanerpes carolinus*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), and Northern Cardinal (*Cardinalis cardinalis*; Beddall, 1963; Ellison, 1993; Jackson & Davis, 1998; Kirchman & Schneider, 2015). While there is some evidence that distributions for at least some of these species are limited by climate (Root, 1988; Mehlman, 1997), increased anthropogenic supplemental feeding, and land-use changes may also have contributed to their increasing trends. For these species, demographic growth and overall geographic expansion have likely contributed to their ability to track climate change northward. However, greater colonization of BBS routes in colder and drier conditions (i.e., in the CCOQ) compared to elsewhere for increasing species indicates

that improved tracking is not simply the result of geographic expansion, but colonization specifically of sites within historical climate niches.

On the other hand, there is compelling evidence that changes in climate can directly influence population trends. In a recent study, Stephens *et al.* (2016) showed that North American and European bird species disadvantaged by climate change in the previous 30 years (those showing a decrease in the availability of suitable climate conditions) have declined more than species favored by climate change (facing an increase in the availability of suitable climate conditions). However, it is safe to say many factors other than climate change are surely impacting population status and trends. All but one of the 23 declining species in our study are at least partially migratory, and factors throughout the annual cycle may be impacting population trends for these species (Robbins *et al.*, 1989; Norris *et al.*, 2004). It is therefore unlikely that an inability to track climate changes on the breeding grounds is solely responsible for observed declining trends. Instead, demographic and geographic contraction of ranges and a limited supply of dispersers could reduce ability to track climate change (Anderson *et al.*, 2009). Another possibility is that species that prefer habitats unavailable further north of their current distribution due to human development (Bateman *et al.*, 2016), or those that face barriers to dispersal will be unable to track climate conditions northward. While we do not quantitatively analyze tracking across habitat types, our list of declining and lagging species is an ecologically diverse set with associations in a variety of habitat types (Supporting information). If lagging is the result of overall population declines and a lack of dispersers, general conservation efforts to stabilize declining populations including efforts to protect current habitats on breeding and wintering grounds and along migratory pathways may indirectly improve species' resilience to climate change. Conversely, a positive feedback between declines and lagging may lead to increased extinction risk for species declining for reasons unrelated to climate change.

Our results have important implications for predicting future species distributions using a correlative modeling approach (Hijmans & Graham, 2006). These models are used to assess extinction risk and conservation priority in the face of climate change (Langham *et al.*, 2015), but assume niche conservatism and often fail to account for any lag or limits to dispersal (Soberón & Nakamura, 2009; Wiens *et al.*, 2009). While many researchers have stressed the importance of incorporating dispersal ability in predictive distribution models (Pearson & Dawson, 2003), this is rarely fully considered for migratory birds which are usually assumed to be sufficiently mobile. Yet our results demonstrate that

even for this vagile group, geographic lagging is a common pattern in climate change responses (Devictor *et al.*, 2008; La Sorte & Jetz, 2012). Predictive models based on current occurrence–climate correlations are likely overpredicting future distribution for declining species, and underpredicting for increasing species, potentially influencing assessments of conservation status and extinction risk (Langham *et al.*, 2015). Population trends and associated changes in realized climate niche, therefore, introduce a source of uncertainty for distribution models not previously considered (Heikkinen *et al.*, 2006; Wiens *et al.*, 2009). Future efforts to incorporate population trends and changes in realized niche into predictive distribution models may improve their utility in conservation planning.

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References

- Anderson BJ, Akçakaya HR, Araújo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society of London Series B*, **276**, 1415–1420.
- Auer SK, King DI (2014) Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Global Ecology and Biogeography*, **23**, 867–875.
- Bateman BL, Pidgeon AM, Radeloff VC, Vanderwal J, Thogmartin WE, Vavrus SJ, Heglund PJ (2016) The pace of past climate change vs. potential bird distributions and land use in the United States. *Global Change Biology*, **22**, 1130–1144.
- Beddall BG (1963) Range expansion of the cardinal and other birds in the northeastern states. *Wilson Bulletin*, **75**, 140–158.
- Bertrand R, Lenoir J, Piedallu C *et al.* (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–520.
- Broennimann O, Fitzpatrick MC, Pearman PB *et al.* (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481–497.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **332**, 258–261.
- Cury PM, Boyd IL, Bonhommeau S *et al.* (2012) Global seabird response to forage fish depletion – one-third for the birds. *Science*, **334**, 1703–1706.
- Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London Series B*, **275**, 2743–2748.
- Ellison WF (1993) Historical patterns of vagrancy by Blue-gray Gnatcatchers in New England. *Journal of the Field Ornithology*, **64**, 358–366.
- Foden W, Midgley GF, Hughes G *et al.* (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions*, **13**, 645–653.
- Foster JR, D'Amato AW (2015) Montane forest ecotones moved downslope in northeastern USA in spite of warming between 1984 and 2011. *Global Change Biology*, **21**, 4497–4507.
- Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology and Evolution*, **29**, 260–269.
- Halpin PN (1997) Global climate change and natural-area protection: management responses and research directions. *Ecological Applications*, **7**, 828–843.
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.
- Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, **34**, 623–642.
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 751–777.
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.
- Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.
- Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Hijmans RJ, Phillips S, Leathwick J, Elith J (2014) dismo: Species distribution modeling. R package version 1.0-5. <http://CRAN.R-project.org/package=dismo>
- Hill JK, Thomas CD, Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology*, **65**, 725–735.
- Hitch AT, Leberg PI (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, **21**, 534–539.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.
- Jackson JA, Davis WE Jr (1998) Range expansion of the Red-bellied Woodpecker. *Bird Observer*, **26**, 4–12.
- Jones SJ, Lima FP, Wetthey DS (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography*, **37**, 2243–2259.
- Karr KA, Fujita R, Halpern BS *et al.* (2015) Thresholds in Caribbean coral reefs: implications for ecosystem-based fishery management. *Journal of Applied Ecology*, **52**, 402–412.
- Keith DA, Akçakaya HR, Thuiller W *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic habitat models. *Biology Letters*, **4**, 560–563.
- Keppel G, Van Niel KP, Wardell-Johnson GW *et al.* (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, **21**, 393–404.
- Killick R, Eckerly IA (2014) changepoint: an R package for changepoint analysis. *Journal of Statistical Software*, **58**, 1–19.
- Kirchman JJ, Schneider KJ (2015) Range expansion and the breakdown of Bergmann's Rule in red-bellied woodpeckers (*Melanerpes carolinus*). *The Wilson Journal of Ornithology*, **126**, 236–248.
- La Sorte FA, Jetz W (2012) Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, **81**, 914–925.
- La Sorte FA, Thompson FR III (2007) Poleward shifts in winter ranges of North American birds. *Ecology*, **88**, 1803–1812.
- Langham GM, Schuetz JG, Distler T, Soykan CU, Wilsey C (2015) Conservation status of North American birds in the face of future climate change. *PLoS ONE*, **10**, e0135350.
- Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography*, **20**, 58–72.
- Link WA, Sauer JR (2002) A hierarchical analysis of population change with application to cerulean warblers. *Ecology*, **83**, 2832–2840.
- McLachlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, **21**, 297–302.
- Mehlman DW (1997) Changes in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614–624.
- Menéndez R, Megias AG, Hill JK *et al.* (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society Series B, Biological Sciences*, **273**, 1465–1470.
- Morecroft MD, Crock HQP, Duffield SJ, Macgregor NA (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547–551.
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.

- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliff LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of Royal Society of London Series B*, **271**, 59–64.
- Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Pauli H, Gottfried M, Grabherr G (1996) Effects of climate change on mountain ecosystems – upward shifting alpine plants. *World Resource Review*, **8**, 382–390.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.
- Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.
- Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.
- Petitpierre B, Kueffer C, Borenmann O, Randin C, Daehler C, Guisan A (2012) Climate niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344–1348.
- Pulliam HR (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ralston J, Kirchman JJ (2013) Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in blackpoll warblers (*Setophaga striata*). *Conservation Genetics*, **14**, 543–555.
- Ralston J, DeLuca WV, Feldman RE, King DI (2016) Realized climate niche breadth varies with population trend and mediates the relationship between abundance and distribution. *Global Ecology and Biogeography*, **25**, 1173–1180.
- Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences of the United States of America*, **86**, 7658–7662.
- Root T (1988) Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330–339.
- Sauer JR, Link WA (2011) Analysis of the North American breeding bird survey using hierarchical models. *The Auk*, **128**, 87–98.
- Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ Jr, Link WA (2014). The North American Breeding Bird Survey, Results and Analysis 1966–2013. Version 01.30.2015 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA
- Schuetz JG, Langham GM, Soykan CU, Wilsey CB, Auer T, Sanchez CC (2015) Making spatial prioritizations robust to climate change uncertainties: a case study with North American birds. *Ecological Applications*, **25**, 1819–1831.
- Smith RIL (1994) Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia*, **99**, 322–328.
- Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19644–19650.
- Stephens PA, Mason LR, Green RE *et al.* (2016) Consistent response of bird populations to climate change on two continents. *Science*, **352**, 84–87.
- Sutton WB, Barrett K, Moody AT, Loftin CS, deMaynadier PG, Nanjappa P (2015) Predicted changes in climatic niche and climate refugia of conservation priority salamander species in the Northeastern United States. *Forests*, **6**, 1–26.
- Tayleur C, Caplat P, Massimino D, Johnston A, Jonzén N, Smith HG, Lindström A (2015) Swedish birds are tracking temperature but not rainfall: evidence from a decade of abundance changes. *Global Ecology and Biogeography*, **24**, 859–872.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.
- Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19637–19643.
- Tingley MW, Koo M, Moritz C, Rush AC, Beissinger SR (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, **18**, 3279–3290.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.
- Wiens JA, Stalberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19729–19736.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.
- Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters*, **38**, L04601.

Supporting Information

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

Appendix S1. The effect of prevalence (number of occurrences) on niche shift metric estimates.

Appendix S2. Niche metrics for null model of geographic lagging

Appendix S3. Determining the effects of length of time periods used for niche estimation.

Table S1. Forty six species of North American breeding birds and their population trends in abundance as reported by the North American Breeding Bird Survey, Niche shift metrics niche expansion and niche unfilling, and climate response indices Expansion Index and Lagging Index.

Appendix S4. R Script.