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CONCEPT PAPER

Realized climate niche breadth varies with population trend and distribution in North American birds

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ABSTRACT

Aim Ecological niche theory states that realized niche breadth should increase with population growth. This relationship has been studied extensively in the context of density-dependent habitat selection, and there is evidence that animal populations at higher density occupy a wider range of vegetation types. To our knowledge, no previous studies have investigated the relationship between population growth and climate niche breadth (i.e. the range of climatic conditions occupied). Here we aim to estimate the influence of population trend, as well as changes in distribution, on realized climate niche breadth.

Location North America.

Methods We estimated changes in realized climate niche breadth and distribution between 1980 and 2012 for 46 bird species using data from the North American Breeding Bird Survey (BBS) and standard ecological niche modelling techniques. We analysed changes in niche breadth in relation to population trends and distributional changes from the BBS for these same species.

Results Changes in realized climate niche breadth were significantly and positively associated with population growth, as reflected by BBS population trends, and with changes in distributional extent. Using variance partitioning, we showed that 44.2% of the variation in change in niche breadth can be explained by population trend, and that roughly half of this was independent of changes in distribution.

Conclusions Realized climate niche breadth is variable on an ecological time-scale as a function of population trend. Mechanisms associated with changes in distribution and those acting within current species range limits appear to be equally important in driving this relationship. Observed changes in niche breadth may violate distribution modelling assumptions of niche conservatism. Studying how population growth influences realized climate niche breadth is therefore important for understanding dynamic species distributions, responses to climate change and our ability to model future species distributions.

Keywords

Abundance, Breeding Bird Survey, Grinnellian niche, Maxent, species distribution.

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INTRODUCTION

The theory that niche breadth expands with population growth is a foundational concept in ecology. As abundance increases, density-dependent mechanisms force individuals into suboptimal sites, resulting in the population occupying an increasing breadth of conditions (Fretwell & Lucas, 1969; Vandermeer, 1972). This idea is widely accepted in the framework of bionomic niche components (i.e. consumable resources subject to competition; Hutchinson, 1978) such as habitat, with several studies demonstrating that animal populations at high density occupy a more diverse set of vegetation types (Morse, 1976; Cody, 1985; Kie & Bowyer, 1999). However, it is not known whether this rule also applies to scenopoetic niche components (i.e. non-consumable environmental conditions; Hutchinson, 1978) such as climate niche. Many studies operate under the assumption that climate niche is conserved within species so that expanding populations or those shifting in response to climate change will geographically track their climate niche (Devictor *et al.*, 2008; Tingley *et al.*, 2009). While *fundamental* niche (i.e. the conditions suitable for a species; Hutchinson, 1957) may well be conserved, we are interested in whether population trends drive shifts in *realized* climate niche (i.e. the climate conditions that are actually occupied), similar to those shifts observed in studies of non-climatic niche breadth. For example, if increasing population trends drive geographical expansion into new climatic conditions, or if population declines cause range contractions away from previously occupied niche space, population trend would be affecting realized climate niche breadth via changes in distribution. Additionally, if increasing populations are more likely to persist at sites of occurrence despite modern climate change, population growth could again lead to changes in realized climate niche breadth, in this case potentially independent of changes in total distributional extent.

Previous studies have investigated the relationship between niche breadth, abundance and distribution in animal species, but they all either focus on non-climatic niche components, rely on interspecific comparisons and/or assume the niche to be fixed within species (Heino, 2005; Hurlbert & White, 2007; Green *et al.*, 2008; Jiguet *et al.*, 2013; Sheth *et al.*, 2014). By treating niche breadth as static within species over time, niche breadth has functioned only as an independent, explanatory, latent variable that contributes to the positive correlation between local species abundance and geographical distribution (hereafter the 'distribution–abundance relationship' *sensu* Borregaard & Rahbek, 2010) by separately influencing abundance and distribution. Niche breadth is often cited as an important mechanism in shaping the distribution–abundance relationship (Gaston *et al.*, 1997; Borregaard & Rahbek, 2010), but only in the context of density-dependent habitat selection have studies allowed for niche breadth to vary within species over time and play a more integral role (i.e. not as a latent variable).

Ecological niche models, also known as species distribution models, can be used to correlate species occurrences with a combination of biotic or abiotic variables to quantify occupied niche space (Peterson, 2006), and have been valuable in exploring the relationship between climate niche breadth and abundance or distribution (Banta *et al.*, 2012; Sheth *et al.*, 2014). These models can also be used to predict a species' distributional response to climate change by projecting the estimated climate niche onto predicted future conditions (Pearson & Dawson, 2003; Hijmans & Graham, 2006). However, if population trends and changes in distribution are associated with changes in realized climate niche breadth, predictive models that fail to account for this risk confounding climate influences with population trends. Thus, study of the effects of population trends on realized climate niche breadth and distribution is key to our understanding of dynamic species distributions and responses to climate change and our ability to model species distributions into the future. We tested whether population trends and changes in distribution were associated with changes in realized climate niche breadth by analysing 33 years of data for North American breeding birds.

METHODS

Population trends

Publicly available estimates of population trends were obtained from the North American Breeding Bird Survey (BBS) for 1980–2012 (Sauer *et al.*, 2014). The BBS is a roadside survey in which trained volunteers record species detected at 50 points along 40-km routes, each surveyed for 3 min. The BBS covers the majority of the conterminous USA, as well as Alaska and portions of southern and maritime Canada (see Appendix S1 in Supporting Information). We began with 1980 because we could obtain at least 30 years of population data, but prior to 1980 the number of surveyed routes in common with 2012 decreases substantially. Trends for each species are estimated from yearly population indices of abundance (the sum of the counts from the 50 points along a route) using a hierarchical model in which observer effects and population parameters are able to vary regionally and are estimated at multiple geographical scales (Link & Sauer, 2002). Here we use 'trends' to refer to the average rate of yearly population change during the study period (Link & Sauer, 2002), which incorporates changes in total population size and changes in local (route level) abundances. For our analyses we used reported 'survey-wide' trends that are estimated across the entire BBS study region of the USA and Canada (Sauer *et al.*, 2014). We obtained trends for all species with the highest BBS credibility measure (Sauer *et al.*, 2014). We limited our analysis to species with distributions that were at least 70% covered by the BBS so that we captured the majority of the climate niche for each species analysed. This excludes species predominantly distributed at high latitudes whose occupied environmental conditions are not adequately sampled by the BBS (Elith *et al.*, 2006; Phillips *et al.*, 2009). Coverage of species distributions by the BBS was determined by comparing a minimum convex polygon encompassing all BBS routes surveyed in 1980 or 2012 with digital species range maps obtained from BirdLife International (BirdLife International and NatureServe, 2012).

Climate niche breadth

We estimated the climatic niche for each species for two time periods: 1980–82 (hereafter ‘1980’) and 2010–12 (hereafter ‘2010’) using Maxent, a presence–background model which compares environmental covariates at occurrences and background points to determine variables of importance and estimate geographical distribution (Phillips *et al*., 2006; Elith *et al*., 2011). Maxent performs well in comparison with other distribution modelling methods (Elith *et al*., 2006), is among the preferred software for ecologists modelling species distributions (Ahmed *et al*., 2015), and has been used in recent studies quantifying climate niche breadth in relation to species distributions (Banta *et al*., 2012; Sheth *et al*., 2014). To choose the most appropriate settings in Maxent for each species we used the R package ENMeval (Muscarella *et al*., 2014), which compares and provides values of the Akaike information criterion corrected for small sample size (AICc) for Maxent models with varying model settings. We compared default settings and a total of six alternative models that varied in the use of feature classes (linear, quadratic, hinge) and the regularization multiplier value (0.5, 1, 2), following recommendations from Merow *et al.* (2013; Appendix S2). We modelled the climate niche for each species in Maxent using the model with the lowest AICc from ENMeval analyses using the ‘checkerboard1’ method of data partitioning (Muscarella *et al*., 2014). Yackulic*et al.* (2013) note that while Maxent is a potentially powerful tool, biased sampling and failure to account for detection probabilities may compromise analyses. In our case, the hierarchical models used to estimate population trends from BBS data account for observer effects and covariates of detection, and the distribution of BBS routes is fairly representative of the climate breadth of the study region (Link & Sauer, 2002; Sauer & Link, 2011). Additionally we calculated a bias surface for each time period as the sum of the number of BBS routes surveyed within each climate grid cell during that time period. Bias surfaces were used in Maxent analyses to account for any geographical differences in the densities of BBS routes potentially leading to bias in the climate space sampled (Elith *et al*., 2011). Nonetheless, like all presence-only models, we must assume for our Maxent estimates of climate niche that environmental covariates of presence do not also influence detection probabilities (Yackulic *et al*., 2013).

Occurrences for each species were obtained from raw BBS count data. To reduce the influence of annual variability and render analyses more tractable, we estimated the ‘1980’ niche for each species using occurrences and climate data from 1980–82, and ‘2012’ niches were estimated using occurrences and climate data from 2010–12. To be counted as an occurrence, a species needed to be detected only once in the 3-year window of each time period. To ensure that we did not miss quantifying parts of the realized climatic niche with only 3 years of occurrence records, we also estimated climate niche using 4- and 5-year windows for each time period. All results were consistent regardless of the number of years in each time period (Appendix S3), so we only report the results from the 3-year window. We used eight bioclimatic variables in the niche modelling: annual mean temperature, temperature seasonality (standard deviation × 100), maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation seasonality (coefficient of variation), precipitation of the wettest quarter and precipitation of the driest quarter. These bioclimatic variables were calculated from Climate Research Unit monthly climate data (Harris *et al*., 2014) at a 0.5° resolution using the R package dismo (Hijmans *et al*., 2014). Climate data corresponded to each of the occurrence time periods. Bioclimatic variables were mostly uncorrelated with one another at surveyed BBS sites in 1980 and in 2012 (21/28 r-values in the correlation matrix, <0.60 in each time period). We calculated climate niche breadth by using ENM Tools to apply Levins’ inverse concentration metric (Levins, 1968) to continuous climate suitability scores from raw Maxent outputs for each species and time period (Nakazato *et al*., 2010). Levins’ inverse concentration was calculated using the equation:

$$\frac{\dfrac{1}{\sum_{i=1}^{n}\left(\dfrac{p_i}{\Sigma_i^n p_i}\right)^2}-1}{n}$$

where p_i is the climate suitability of each grid cell, i, and n is the number of grid cells. Estimates of niche breadth are scaled by the suitability of all available sites, so that the minimum possible niche breadth of 0 represents high specificity with only one geographical grid cell with a non-zero climate suitability, and the maximum possible niche breadth of 1 represents equal suitability across all available grid cells. Change in niche breadth for each species is calculated as a percentage of the 1980 niche breadth.

Distribution

We used BBS occurrence data to estimate the distributional extent of each species in each time period. Distributional extent was calculated in the R package adehabitatHR (Calenge, 2006) as the area of a minimum convex polygon surrounding 95% of occurrences. To avoid bias from differences in the number and location of surveyed BBS routes across years, we only used BBS routes surveyed in both time periods ($n = 1584$) to estimate distributional extent. We report changes in distribution as the percentage changes in the 1980 values. Because the density of BBS routes varies between western and eastern North America (Appendix S1), real distributional changes may manifest differently in BBS data for species predominantly located in different regions. To ensure that our analyses were not compromised by including species from both regions, we also analysed data with the small number of predominantly western species ($n = 2$) removed, but found no effect on the relationship between trend and change in distribution (Appendix S1).

Statistical analyses

Because we were unsure how the number of occurrences would influence estimates of niche breadth, we explored the relationship between population trend and change in niche breadth using simple linear regression while limiting the analysis to species with an increasingly restrictive sample size. We found that analyses including species with smaller numbers of occurrences generally had lower R^2 values, suggesting to us that climate niche breadth was unreliably estimated for these species (Appendix S4). We therefore limit all further statistical analyses to 46 species with at least 600 occurrences in both 1980 and 2012 time periods (Appendix S4). We used multiple regression implemented in R version 3.1.2 (R Core Team, 2014) to determine the effects of population trend and change in distributional extent on change in realized climate niche breadth. The assumption of non-collinearity between independent variables was tested by calculating the variance inflation factor (VIF) of our models. We use the value of R^2 from the multiple regression to indicate the total variation in change in niche breadth attributable to population trend and change in distribution. We then used variance partitioning to determine the importance of various mechanistic pathways in contributing to changes in climate niche breadth. We partitioned variance from the multiple regression into five components as follows using the R package vegan (Oksanen *et al.*, 2014): (1) we calculated the total variation explained by population trend (R^2_t), where R^2_t represents all variation in change in niche breadth attributable to population trend, including mechanisms independent of and mediated by changes in distributional extent; (2) we calculated the variation uniquely explained by trend independent of changes in distribution ($R^2_{t|d}$); (3) we calculated the variation explained by trend as mediated by changes in distribution ($R^2_{t[d]}$), where $R^2_{t[d]}$ represents the mechanisms by which trend influences niche breadth via changes in distributional extent; similarly we calculate (4) the total variation explained by distribution (R^2_d); and (5) the variation uniquely explained by distribution independent of population trend ($R^2_{d|t}$).

RESULTS

We obtained trends for 46 species of North American breeding birds which met inclusion criteria (Appendix S5). Default Maxent settings received the lowest AICc scores in ENMeval for 35 (76.1%) and 39 (84.8%) of these species in the 1980 and 2012 time periods, respectively (Appendix S5). Ecological niche models for each of these species in each time period generally performed well, with a mean area under the receiver operating curve (AUC) of 0.919, a minimum AUC across all species of 0.807 (but see Lobo *et al.*, 2008, for caveats about the use of AUC to asses predictive model performance) and a mean regularized training gain of 0.35. This regularized gain indicates that an average occurrence has a climate suitability score 1.42 (or $e^{0.35}$) times greater than an average background site. The VIF was low for population trend and change in distributional extent (1.29) indicating non-collinearity. Multiple regression indicated that change in realized climate niche breadth was significantly and positively influenced by population trend ($\beta = 0.55$, $P < 0.001$; Fig. 1a), and by change in distributional extent ($\beta = 0.25$, $P = 0.043$; Fig. 1b). A large percentage of the observed variation in change in realized climate niche breadth was explained by population trend ($R^2_t = 0.442$; Fig. 2). Much of this variation was shared with distribution ($R^2_{t[d]} = 0.209$), though we found that trend also explained a roughly equal proportion of the variation in realized climate niche breadth independent of changes in total distributional extent ($R^2_{t|d} = 0.233$; Fig. 2).

DISCUSSION

We have demonstrated that realized climate niche breadth changes within bird species through time as a function of population trend. This expands long-standing ecological niche theory that occupied niche breadth increases with population growth (Vandermeer, 1972). Previous studies have supported this in the context of non-climatic niche breadth, for example with density-dependent habitat selection (Cody, 1985; Kie & Bowyer, 1999), but to our knowledge ours is the first to demonstrate that it also applies to non-consumable, scenopoetic variables such as climate niche breadth. Niche breadth has been used as a static, explanatory variable of population trends (Green *et al.*, 2008; Jiguet *et al.*, 2013) or geographical distribution (Sheth *et al.*, 2014), or as a latent variable in the distribution–abundance relationship (Brown, 1984; Heino *et al.*, 2008; Borregaard & Rahbek, 2010). By treating climate niche breadth as dynamic, we were able to document for the first time its direct relationship with population trend.

A large proportion of our study species were declining (50%), had shrinking geographical distributions (52%) and experienced decreases in realized climate niche breadth (63%). Wide-scale population declines in North American birds have been under study for several decades (e.g. Robbins *et al.*, 1989), and remain an ongoing conservation concern. Drivers of declines in bird populations include land-use change, climate change (Waite & Strickland, 2006), disease (LaDeau *et al.*, 2007), feral cats (Loss *et al.*, 2013) and additional stressors throughout the annual cycle of migratory species (Rappole & McDonald, 1994). While it is beyond the scope of this paper to address each of these drivers of population decline, we note here that population-level stressors may have impacts on aspect of the species ecology not previously explored, namely realized climate niche breadth.

While unravelling the mechanisms by which population trends influence realized climate niche breadth will require further investigation, our results can shed light on the relative importance of potential mechanistic pathways. Our results indicate that much of the influence of population trends on climate niche breadth is mediated by changes in distributional extent (Fig. 2). This includes several possible mechanisms. First, climate variables delimit range peripheries (Root, 1988) and determine habitat suitability (Smith *et al.*, 2010) for many species. Thus, as individuals are pushed to

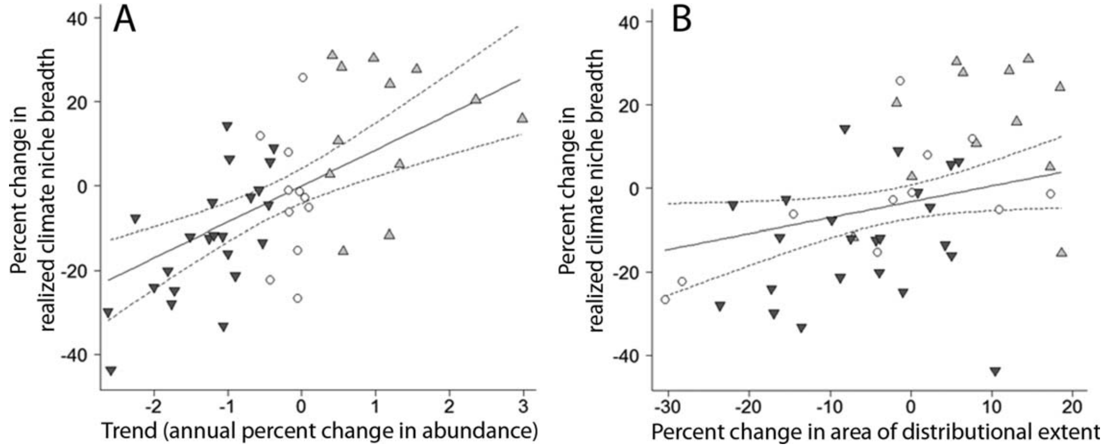

Figure 1 Relationships between change in realized climate niche breadth for 46 bird species and (a) population trends estimated from the North American Breeding Bird Survey and (b) change in distributional extent. Light grey upward triangles indicate species with significantly positive trends, open circles indicate species with trends not significantly different from zero and dark grey downward triangles indicate species with significantly negative trends. Black lines represents the predicted relationship with 95% confidence intervals between change in realized climate niche breadth and the variable of interest according to the multiple regression model while holding the other independent variable at its mean. Change in realized climate niche breadth is positively and significantly influenced by both population trend and change in distributional extent.

range peripheries and into new habitats via well-described density-dependent mechanisms they may secondarily be colonizing new climate space. Even without competitive interactions implicit in many density-dependent models (Fretwell & Lucas, 1969; Vandermeer, 1972), populations may passively diffuse from areas of high density to areas of lower density. This may similarly result in the secondary colonization of new climate space. Conversely, range contractions associated with population declines would decrease the breadth of climate conditions occupied by a species. Second, metapopulation theory predicts that local extinctions will cause species to occupy only a subset of available suitable conditions at any given time, and dispersal from sources to sinks may result in the occupation of unsuitable conditions (Pulliam, 1988, 2000). Increasing populations are more likely to act as sources, providing higher numbers of dispersers and increasing the colonization of new conditions while decreasing the probability of local extinction. This would result in species with increasing trends occupying a broader realized niche more closely resembling, or perhaps exceeding, the fundamental niche breadth compared with species with decreasing trends (Pulliam, 2000). Third, climate change may simultaneously influence population trends, realized niche breadth and geographical distribution. If climate change causes population declines and range contractions on the southern periphery of a species range (Waite & Strickland, 2006) while northward expansion is lagging behind climate (Devictor *et al.*, 2008), or if southern peripheries shift faster than northern peripheries (Zuckerberg *et al.*, 2009), geographical changes will be associated with population declines and a reduction in realized climate niche breadth.

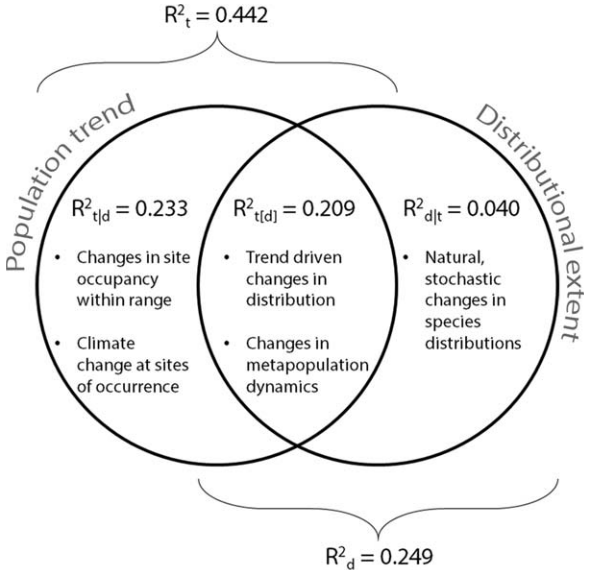

Figure 2 Variance partitioning from multiple regression of change in climate niche breadth as a function of population trend and change in distributional extent. The values in each space represent the percentage of variation in change in realized climate niche breadth uniquely attributable to population trend ($R^2_{t|d}$), change in distributional extent ($R^2_{d|t}$), or the shared variance from these variables ($R^2_{t[d]}$). The text in each area shows possible mechanisms associated with partitioned variance.

Each of the above mechanisms is explicitly geographical; however, our results suggest that population trend is also capable of influencing niche breadth independent of changes in total distributional extent. One way this could occur is from a combination of climate change at sites of historic occurrence and variation in the rate at which species go extinct from these changing sites. If increasing species are more likely to persist at historic sites of occurrence despite changing climates, they may show greater increase in realized climate niche breadth without the colonization of new sites. Similarly, if increasing species are differentially located at sites that have become more variable in climate over the study period, this would result in an increase in niche breadth independent of any distributional changes. Interestingly, many of our study species exhibited a decrease in realized climate niche breadth, despite stable or increasing trends (10/46 species, 21.7%; Fig. 1a) or geographically expanding populations (9/46 species, 19.6%; Fig. 1b). This demonstrates that *in situ* climate change is capable of influencing realized climate niche breadth independent of changes in distribution or trend. We are currently working on additional analyses to further investigate the relationship between ongoing climate change and changes in climate niche breadth for these same species of North American birds. Lastly, changes in climate niche breadth could occur via changes in site occupancy within species current distributions. For example, if a declining species disappears from a number of climatically suboptimal sites within its range this would be observed in our data as a declining trend associated with a decrease in realized climate niche breadth, but without a change in overall distributional extent.

Regardless of the mechanisms responsible, the observation that population trend influences climate niche breadth has important implications for understanding dynamic species distributions and modelling species responses to climate change. Modelling species distributions has become an increasingly valuable ecological approach, especially given anthropogenic changes to the landscape and climate (Elith *et al.*, 2011; Bellard *et al.*, 2012). Typically these models rely heavily or solely on climatic variables to estimate a species niche, which can then be applied to modelled future climates to predict future distributions (Hijmans & Graham, 2006). An important assumption underlying these predictive models is niche conservatism, i.e. that species climate niche does not change over time. It is therefore commonly assumed that as climates change, species distributions will shift to geographically track their climate niche (Devictor *et al.*, 2008; Tingley *et al.*, 2009). However, our results indicate that changes in geographical distribution are not always the result of niche tracking, but instead may result in changes in niche breadth (Fig. 1b). While the term ‘niche conservatism’ is generally reserved to describe a lack of changes in the fundamental niche on an evolutionary time-scale (Peterson *et al.*, 1999), our results demonstrate that changes in realized climate niche on an ecological time-scale are quite possible and may violate the assumptions of distribution modelling. McFarland *et al.* (2014) demonstrated that for a species with an increasing trend, performance of predictive distribution models decreased over time, which we argue is likely to be a result of changes in niche breadth over the study period. Predictive models may underestimate future distributions for increasing species if these species broaden their realized climate niche, or overestimate future distributions of declining species. Thus, models or analyses of climate scenarios that fail to account for population trends may confound the influences of population trend with climate responses. Future work should focus on evaluating the performance of distribution models given unstable population trends (McFarland *et al.*, 2014) and the development of predictive distribution modelling techniques that account for population trends and potential changes in realized niche.

If density-dependent niche occupancy models (Fretwell & Lucas, 1969; Vandermeer, 1972) apply to climate niches in similar ways as habitat use, which we argue they do, we can hypothesize that climate niche space newly occupied by increasing species is suboptimal compared with historically occupied niche space. Similarly, unfilled niche space for declining species may be suboptimal compared with niche space that is still being occupied. Understanding how fitness and reproductive success vary across climate niche space could be an important avenue for future investigation, as it has been with density-dependent habitat selection (Morris, 1989; Sillett *et al.*, 2004). For example, if populations in newly occupied climate niche space represent sinks where reproductive success is reduced, a negative feedback on population growth may occur, resulting in a buffer effect and population regulation (Brown, 1969; Pulliam, 1988). While others have defined ecological niche as the set of conditions under which the intrinsic rate of increase is non-negative (Sheth *et al.*, 2014), we make no statements here about fitness or growth rate and instead use the range of conditions occupied to define realized niche, as is consistent with ecological niche modelling (Pearson & Dawson, 2003; Soberón & Peterson, 2005) and niche theory (Pulliam, 2000). This is an important distinction to make given that species distributions are dynamic, and that the 1980 and 2012 niche models we analyse represent only two time periods of ever-changing species distributions (Manning *et al.*, 2014). Our results and conclusions contribute to the understanding of distribution dynamics by highlighting the importance of population trends and associated changes in realized climate niches. We suggest that future studies focused on population regulation, dynamic species distributions, responses to climate change or the distribution–abundance relationship would benefit from considering the effects of population trends on dynamic realized climate niches.

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SUPPORTING INFORMATION

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Additional supporting information may be found in the online version of this article at the publisher's web-site:
Appendix S1 Map of Breeding Bird Survey (BBS) routes, and determining the effects of the distribution of BBS routes.
Appendix S2 ENMeval selection of Maxent settings for each species.
Appendix S3 Determining the effects of time period length on niche estimation.
Appendix S4 The influence of the number of species occurrences on modeled relationships.
Appendix S5 Table of analysed species and species-specific results.

BIOSKETCH

The authors are interested in understanding the processes shaping patterns of abundance and distribution in North American birds, especially with respect to climate change and its relationship with niche breadth and niche tracking. All authors are current or former fellows (JR, WVD) or affiliated investigators (REF, DIK) at the Northeast Climate Science Center, a sector of the US Department of the Interior focused on connecting climate researchers with managers, stakeholders and the public.

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