

Climate change in our backyards: the reshuffling of North America's winter bird communities

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Abstract

Much of the recent changes in North American climate have occurred during the winter months, and as result, overwintering birds represent important sentinels of anthropogenic climate change. While there is mounting evidence that bird populations are responding to a warming climate (e.g., poleward shifts) questions remain as to whether these species-specific responses are resulting in community-wide changes. Here, we test the hypothesis that a changing winter climate should favor the formation of winter bird communities dominated by warm-adapted species. To do this, we quantified changes in community composition using a functional index – the Community Temperature Index (CTI) – which measures the balance between low- and high-temperature dwelling species in a community. Using data from Project FeederWatch, an international citizen science program, we quantified spatiotemporal changes in winter bird communities ($n = 38$ bird species) across eastern North America and tested the influence of changes in winter minimum temperature over a 22-year period. We implemented a jackknife analysis to identify those species most influential in driving changes at the community level and the population dynamics (e.g., extinction or colonization) responsible for these community changes. Since 1990, we found that the winter bird community structure has changed with communities increasingly composed of warm-adapted species. This reshuffling of winter bird communities was strongest in southerly latitudes and driven primarily by local increases in abundance and regional patterns of colonization by southerly birds. CTI tracked patterns of changing winter temperature at different temporal scales ranging from 1 to 35 years. We conclude that a shifting winter climate has provided an opportunity for smaller, southerly distributed species to colonize new regions and promote the formation of unique winter bird assemblages throughout eastern North America.

Keywords: avian ecology, citizen science, climate change, community temperature index, Project FeederWatch, winter warming

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Introduction

Since the 1970s, the climate of North America has undergone rapid changes, with the greatest observed changes occurring during the winter season (Rodenhouse *et al.*, 2009; Hartmann *et al.*, 2013). Although global-mean surface temperatures have shown a reduced increasing linear trend over the past 15 years (Trenberth & Fasullo, 2013), the temperature trend in the Northern Hemisphere remains strongly positive (Cohen *et al.*, 2012; IPCC, 2013). The northern hemispheric winter has demonstrated a shift to milder conditions characterized by less snow cover (especially during early spring) (Brown & Robinson, 2011; Callaghan *et al.*, 2011), more variable and intense precipitation events (Groisman *et al.*, 2005), an attenuating snow season (Choi *et al.*, 2010), and a degrading cryosphere (Liston & Hiemstra, 2011). Climate models predict that global temperatures will continue to rise over the next century and these changes will be the most pronounced

in northerly latitudes (Meehl *et al.*, 2007). For many cold-adapted species, these changing climatic conditions represent a distinct environmental shift during a time of resource scarcity and critical energetic tradeoffs (Williams *et al.*, 2014).

Recent changes in global climate have spurred the search for documenting the ecological fingerprints of climate change (Root *et al.*, 2003; Parmesan, 2006). Two of the most widely cited lines of evidence that species are responding to a warming climate are poleward shifts in species' ranges (Wilson *et al.*, 2005; Hickling *et al.*, 2006; Kelly & Goulden, 2008) and an earlier onset in springtime phenology (e.g., migration, flowering) (e.g., Butler, 2003; Both *et al.*, 2004). Meta-analyses have confirmed the systematic robustness of these fingerprints (Parmesan & Yohe, 2003; Visser & Both, 2005; Thomas, 2010), but many of these impacts are based on single species estimates with highly variable responses ranging from dramatic northward shifts to no change at all. Given this variability, questions remain as to whether these species-level responses result in changes at the community level, and if so, whether these changes are mediated by climate.

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Winter birds have long been considered sentinels of climate change due to their well-studied metabolic capacities and ability to survive and adapt to Northern Hemispheric winters. Throughout North America, the northern range boundaries of many winter birds tend to correlate with isotherms of average minimum temperature (Root, 1988a; Zuckerman *et al.*, 2011), presumably the consequence of species reaching a discrete thermoregulatory ceiling (Root, 1988b). Distributional studies have found that many of these same species have been shifting northward and that milder winter temperatures were a likely driver (Valiela & Bowen, 2003; La Sorte & Thompson, 2007). At a local scale, winter birds often exhibit a number of behavioral adaptations to survive the winter season including the formation of mixed species flocks (Greenberg, 2000). Winter flocking is considered an adaptive strategy to cope with harsh environmental conditions while providing for maximum resource exploitation (Morse, 1970, 1977; Berner & Grubb, 1985). Changes in the composition of winter bird assemblages in response to climate change might impact the composition of these flocks and result in the formation of no analog communities (Williams & Jackson, 2007). So far, the relationship between winter bird distributions and climate constraints tends to focus on individual species and resulting changes in local communities remain poorly studied (but see La Sorte *et al.*, 2009).

The goal of our study was to test the hypothesis that a warming North American winter should favor the formation of winter bird communities increasingly dominated by warm-adapted species. To test this hypothesis, we explored the use of a functional index, the Community Temperature Index (CTI) (Devictor *et al.*, 2008, 2012), which measures the balance between low- and high-temperature dwelling species in a community. CTI is derived from individual species' climatic preferences (Species Temperature Index, STI) as measured by the long-term average temperature experienced by a species over its range. If species are shifting polewards in response to a warming climate, then changes in wintering bird CTI could result from either extirpation-driven retractions along the 'warm' range boundary and/or colonization-driven expansions along the 'cold' range boundary. CTI has been used to document community shifts in Europe for breeding birds (Devictor *et al.*, 2008, 2012; Lindström *et al.*, 2013) and wintering waders (Godet *et al.*, 2011), and has been recommended as a critical biodiversity indicator (Van Swaay *et al.*, 2010). The analysis of changes in CTI alone; however, does not identify which species are most influential in driving changes at the community level or shed light on which population dynamics are driving these changes (e.g., extinction vs. colonization).

Across latitudinal gradients, winter bird assemblages tend to reflect Bergmann's rule of larger-bodied species occupying more northerly latitudes (Ramirez *et al.*, 2008). As such, our second hypothesis was that smaller-bodied species would contribute more strongly to CTI changes because higher surface-area-to-volume ratios make them relatively more sensitive to climatic variability in extreme environments (Sibly *et al.*, 2012). If the winter climate of North America is warming and winter birds are tracking their thermal niche, then we predicted that (i) CTI would increase over time; (ii) CTI would increase most in northerly latitudes due to poleward shifts; (iii) CTI changes would be positively correlated with increasing winter temperatures; and (iv) smaller-bodied species will drive community-wide changes.

Materials and methods

North American winter bird data: Project Feeder Watch

Data on North American winter birds come from Project Feeder Watch (PFW), an international citizen science program operated by the Cornell Lab of Ornithology and Bird Studies Canada. Wells *et al.* (1998) reported complete details of the PFW protocol. From early November to late April, program participants record the maximum number of each species seen from a single location near a supplemental feeding station during periodic 2-day counts. These 2-day count periods are repeated throughout the PFW season and are separated by a minimum of five calendar days. For each count, participants record the number of half-day periods (1, 2, 3, or 4 half days) they spent observing their feeder station during the 2-day count period. More than 10 000 PFW sites are located across the United States and Canada each year. We limited our data to PFW sites located in eastern North America, below 50°N Latitude and east of 100th meridian, and surveyed between November 1989 and April 2011 ($n = 1\,624\,927$ checklists). Data from PFW have been successfully used in several avian studies on infectious disease transmission, climatic constraints, habitat fragmentation, interspecific competition, population changes, and invasive species (e.g., Cooper *et al.*, 2007; Bonter *et al.*, 2010; Zuckerman *et al.*, 2011, 2012).

We selected observations submitted during a 10-week period in the winter season, from 1 December to 8 February, representing the 'core winter' season for overwintering bird species in eastern North America (Zuckerman *et al.*, 2011). To maximize detectability (Zuckerman *et al.*, 2011), we restricted our analysis to sites that contributed at least 3 two-day count periods within the core winter season. Our final data set included 30 994 individual PFW sites that contributed data between the winter of 1989/1990 to 2010/2011 (22 years) (Fig. 1). We aggregated Carolina (*Poecile carolinensis*) and Black-capped Chickadees (*Poecile atricapillus*) observations into a single Chickadee *sp.* to avoid known identification issues (e.g., hybrids and overlapping ranges). Similarly, we aggregated observations for Cooper's hawk (*Accipiter cooperii*)

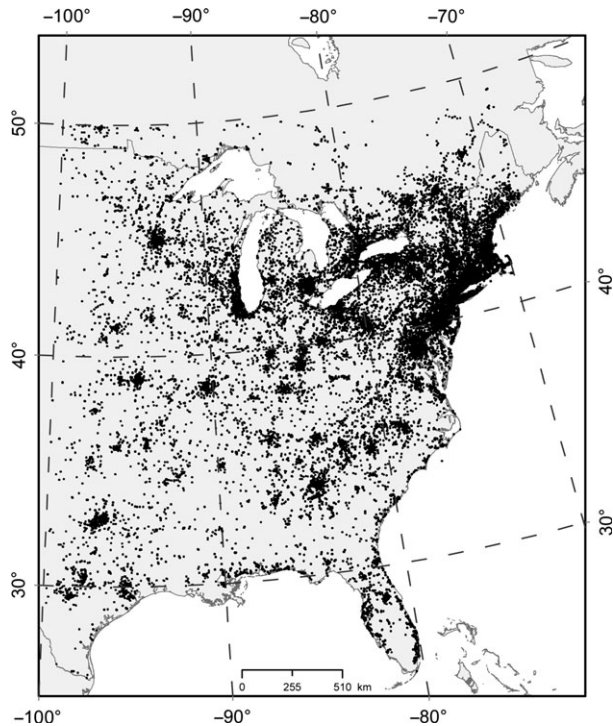


Fig. 1 Spatial distribution of the 30 994 FeederWatch sites surveyed from 1990 to 2011.

and Sharp-shinned Hawk (*Accipiter striatus*) due to identification challenges. Finally, we collapsed the Eastern Towhee (*Pipilo erythrophthalmus*) and Spotted Towhee (*Pipilo maculatus*) into a single Towhee *sp.* because these two species were taxonomically split only recently. Our analysis focused on species that were well-sampled by the PFW protocol and detected at greater than 5% of observations during the sampling period. We also excluded irruptive species [Red-breasted Nuthatch (*Sitta Canadensis*), Common Redpoll (*Acanthis flammea*), and Pine Siskin (*Spinus pinus*)] from our data set. For each species, we calculated the yearly average maximum abundance per feeders (hereafter simply referred as abundance), i.e., the mean of 2-day's maximum counts over the 10-week period. We considered a final subset of 38 species that met our selection criteria. The final subset of species included in this study have core ranges within eastern North America, are readily identifiable, and regularly visit supplemental feeding sites in human-dominated landscapes (making them less likely to be limited by variation in food resources).

Species and community temperature index

We first estimated the temperature profile of each species (Species Temperature Index, STI; Devictor *et al.*, 2008) by computing the average minimum winter temperature (°C) within its range during the winter season. To do this, we used occurrence data from an independent winter bird survey, the North American Christmas Bird Count (CBC; National Audubon Society 2012), collected between 1975 and 1990. CBC surveys are conducted within 12-km radius circles for a period of 24 h

between 14 December and 5 January. We chose 1975 as a start date, because observer effort at CBC circles became relatively consistent at this time (La Sorte & Thompson, 2007). From the 2248 CBC circles, we considered only CBC circles surveyed every year and located within eastern North America between 25 and 50°N latitude ($n = 497$, Figure S1 in Data S1). Survey effort was highly variable within and among the 497 CBC circles, but did not change significantly from 1975 to 2009 (Figure S2 in Data S1). To determine a species' winter range, we considered a species present within a circle if it had been surveyed at least once. Given the strong and temporally consistent heterogeneity in survey effort from 1975 to 1990, we considered that any positive relationship between survey effort and detection probability for each of the 38 species is unlikely to result in any systematic biases for assessing species' ranges. For each species, we calculated the mean monthly minimum temperature (December–January) between 1950 and 2000 where the species was detected. The climate data were generated from the Worldclim database (<http://www.worldclim.org/>) at a 30-arcsec (0.8 km) resolution. This analysis produced a species-specific STI representing the temperature profile of the occupied winter range of that species in eastern North America. Species' temperature indices (STI) range from -7.48 °C [American Tree Sparrow (*Spizella arborea*)] to -3.62 °C [Chipping Sparrow (*Spizella passerina*)] (Table S1 in Data S1). To test for potential biases related to temporal and spatial extents, we also calculated STIs at a different spatial scale (Eastern United States) and used different climate data (PRISM) over a different temporal extent (1975–1990). Estimated STIs were highly correlated, respectively $R = 0.99$ and $R = 0.99$ (Figure S3 in Data S1).

We implemented two different approaches to calculate CTI for each year between 1990 and 2011. We first computed CTI based on occurrence data (hereafter CTI) by averaging the STI of species i occurring at a given PFW site j

$$CTI_j = \frac{\sum_{i=1}^n STI_{i,j}}{n} \quad (1)$$

We then calculated a CTI weighted by species abundance (hereafter weighted CTI), as following:

$$CTI_j = \frac{\sum_{i=1}^n a_{i,j} \times STI_{i,j}}{\sum_{i=1}^n a_{i,j}} \quad (2)$$

where $a_{i,j}$ is the abundance of species i at site j , and n is the total number of species on that site.

Climate data

We used monthly minimum temperature data for the period of 1955–2010 from the PRISM Climate Group (Oregon State University, <http://www.prism.oregonstate.edu/>) gridded data set. PRISM dataset corresponds to data from weather stations interpolated at a 4×4 km grid. We extracted interpolated monthly data at each PFW site using the R package raster (Bivand *et al.*, 2013). As we were primarily interested in minimum winter temperatures, we calculated the yearly average minimum temperature of December–January at each site. Then, at each site and for each year, we estimated the winter

temperature anomaly (i.e., departure from a long-term average) of the 1, 5, 10, 15, 20, 25, 30, and 35 preceding years (5-year moving window). To calculate site-specific winter anomalies, we used the average winter temperature over 1975–1990 as a baseline. Although we calculated trends in CTI over Eastern North America (including southern Canada), we restricted our climate analysis to the Eastern US for exploring the effect of climate on changes in winter bird assemblages because PRISM data were only available for the conterminous United States.

Statistical analysis

We used generalized mixed models (GLMM) (Zuur *et al.*, 2009) to model spatiotemporal changes in the composition of bird communities based on species' temperature preferences, while accounting for the multisite time-series structure of the monitoring program. To account for the nonindependence of our data, we first added 'site' as a random effect to the intercept θ , that is, allowing intercepts to vary between sites. To avoid overconfident estimates (Schielzeth & Forstmeier, 2009), we also included random slopes in the GLMM allowing between-site variation in temporal slopes. We tested for spatial autocorrelation in the residuals of the GLMM using Moran's I correlograms. We found positive autocorrelation in the residuals, and included a first order autoregressive covariance (Zuur *et al.*, 2009), which improved model fit ($\Delta AIC > 2$), although it did not affect results. We included the latitude (Lat) and the longitude (Long) of sites as covariates to estimate geographic trends. The year in which the data were collected was modeled as a continuous variable to assess overall temporal trends (Year). For illustrative purposes, we also estimated interannual variation in CTI by considering Year as a categorical variable instead of continuous. We modeled the average number of half days over the 10-week period at each site

(Effort) as a fixed effect to account for variable sampling effort (Zuckerberg *et al.*, 2011). Using the estimated temporal ($^{\circ}\text{C yr}^{-1}$) and latitudinal ($^{\circ}\text{C km}^{-1}$) trends in CTI, we calculated the ratio between these two measures (respectively, the estimates from Year and Lat as continuous variables in the GLMM) as a proxy for the pace of shifting CTI ($^{\circ}\text{C yr}^{-1} / ^{\circ}\text{C km}^{-1} = \text{km yr}^{-1}$; Loarie *et al.*, 2009; Devictor *et al.*, 2012). To test for latitudinal variation in CTI trends, we estimated the CTI temporal trend within 5-degree latitudinal bands spanning all of eastern North America. For this purpose, the mixed model described above was fitted to the data within each latitudinal band, and Lat was removed from the structure of the GLMMs.

The distribution and intensity of PFW sampling varied across years. To ensure that the covariate relationships estimated using GLMM were not a result of geographic shifts in PFW sampling we performed a randomization procedure (Manly, 2006). The procedure consisted of first randomly selecting a given number of sites each year within a 5° latitudinal band to generate a random data set, which is the quantification of the null-hypothesis that the sampling effort remains constant through time. We then fit the GLMM to this randomly sampled data set and saved the beta estimates. This procedure was repeated 10 000 times. By comparing the observed beta estimates (from the observed data set) with the distribution expected with no change (from the random data), we calculated whether there was a significant probability of a sampling bias (i.e., whether CTI trends were due to sampling geographic change in sampling intensity over 1990–2011).

We tested whether CTI changes were correlated with changes in winter minimum temperature, and predicted that the response of wintering birds to shifting climate space would demonstrate a potential time lag effect (La Sorte & Jetz, 2012). Due to high multicollinearity across moving windows of different time periods, we analyzed short- and long-term time lags by relating CTI to site-specific winter temperature

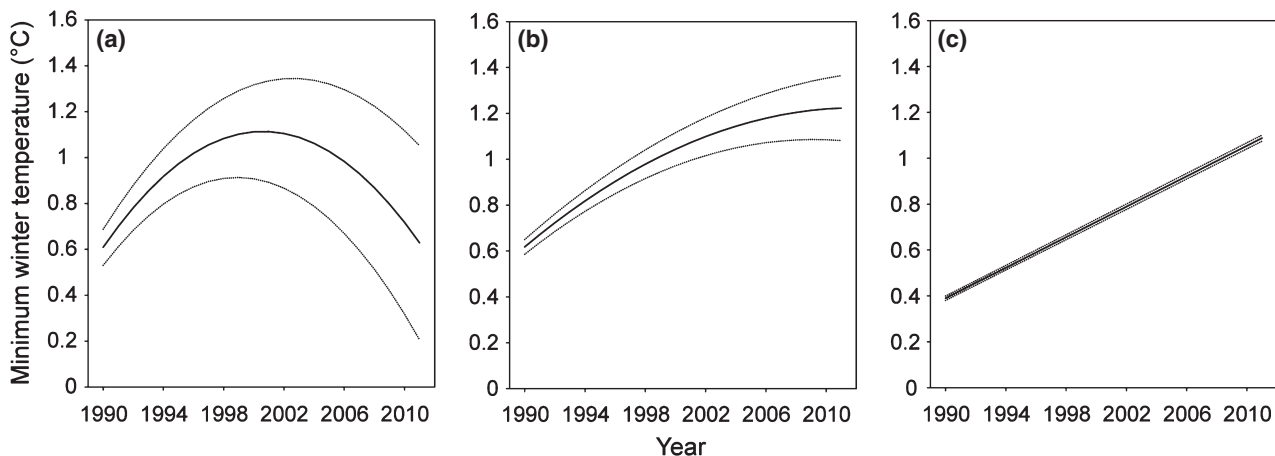


Fig. 2 Trend in minimum winter temperature anomalies of at different time lags of (a) 1 year, (b) 5 years and (c) 35 years, at PFW sites throughout the eastern United States over 1990–2011. Trends were estimated using a generalized linear mixed model with 'site' as a random effect. The dotted lines indicate the 95% confidence interval. For each year, the site-specific anomaly is calculated from the base period 1975–1990. The shorter time windows (a,b) capture a slight lull in climate warming (circa 2004) whereas the longer time window (c) demonstrates the persistent warming trend in winter minimum temperatures.

anomalies of 1, 5, and 35 years earlier. We specified these anomalies as independent variables in the GLMM. For illustrative purposes, we also performed generalized linear mixed models to estimate the trend of temperature anomalies of these different time-moving windows, with 'year' as a fixed effect and 'site' as a random effect (Fig. 2). For the 5 and 35 years moving windows, we considered a quadratic effect of time in the model, as it improved model fit.

To identify which species were most strongly contributing to changes in CTI, we ran a Jackknife procedure (Crowley, 1992). By removing species one by one from the data set, we iteratively recalculated the CTI for each PFW site-year combination and reran the GLMM. For each species, we calculated the percentage difference (C_{sp}) between the 'Year' coefficient from the global model and the jackknife models as a means of assessing species contribution to the community response. If a species contributed toward the CTI trend of the global model C_{sp} will be positive, whereas C_{sp} will be negative if it does not support the overall trend. We performed this analysis using both CTI and weighted CTI over the entire study area and within each latitudinal band.

Following the Jackknife analysis, we tested whether selected life history traits accounted for interspecific variation in C_{sp} . For each species, we estimated the northern latitude of the species' range over the period 1975–1990 (hereafter 'northern boundary'). For this purpose, we used the CBC data (see details above) and calculated the average five percent northernmost latitudes of the species winter distribution. We also used species' average body mass (log-transformed). Body mass for each species came from Dunning (2008) and corresponded to the average across male and female North American specimens. We considered the migratory strategy (temperate migrant *vs.* resident) for each species (Peterjohn & Sauer, 1993). Moreover, to disentangle whether or not changes in CTI was a function of overall population trends, we calculated trends in the proportion of PFW sites visited for each species. We considered the frequency of site visitation as a proxy of regional occupancy, calculated as the number of PFW sites that reported a species at least once over the winter divided by the total number of PFW sites. We used trends in the proportion of sites detected (Occupancy) to examine species contribution to both CTI and weighted CTI, since changes in regional occupancy reflect changes in local abundance across species of varying life history characteristics (Zuckerberg *et al.*, 2009a). Finally, we developed separate Generalized Linear Models (GLM) with a Gaussian error distribution to test the influence of northern range boundary, body mass, migratory strategy, and occupancy on C_{sp} (see Table S2 in Data S2). We standardized all continuous predictor variables, and performed regression diagnostics on the global model using residual plots to check for outliers (Crowley, 2007). We compared models using (i) species that contributed positively toward CTI trends ($C_{sp} > 0$); and (ii) species that strongly contributed toward CTI trends ($C_{sp} > 10\%$). Because some species have a common evolutionary history, the explanatory variables considered (e.g., life history traits) tend to have similar values for closely related species. As a precautionary step, we performed an *ad hoc* analysis to check for phylogenetic relatedness at the family level.

Generalized estimating equations, as described by Paradis & Claude (2002), is one way to test for phylogenetic relatedness, but they are not designed for model selection and comparison approaches as they do not operate in terms of likelihoods. As an alternative, we modeled 'Family' as a random effect within the GLMM. We evaluated all candidate models using an information-theoretic approach (Burnham & Anderson, 2002). For both GLMM and GLM models, we developed an *a priori* set of candidate models (including a global and null model) that we fitted with a maximum likelihood estimator and then

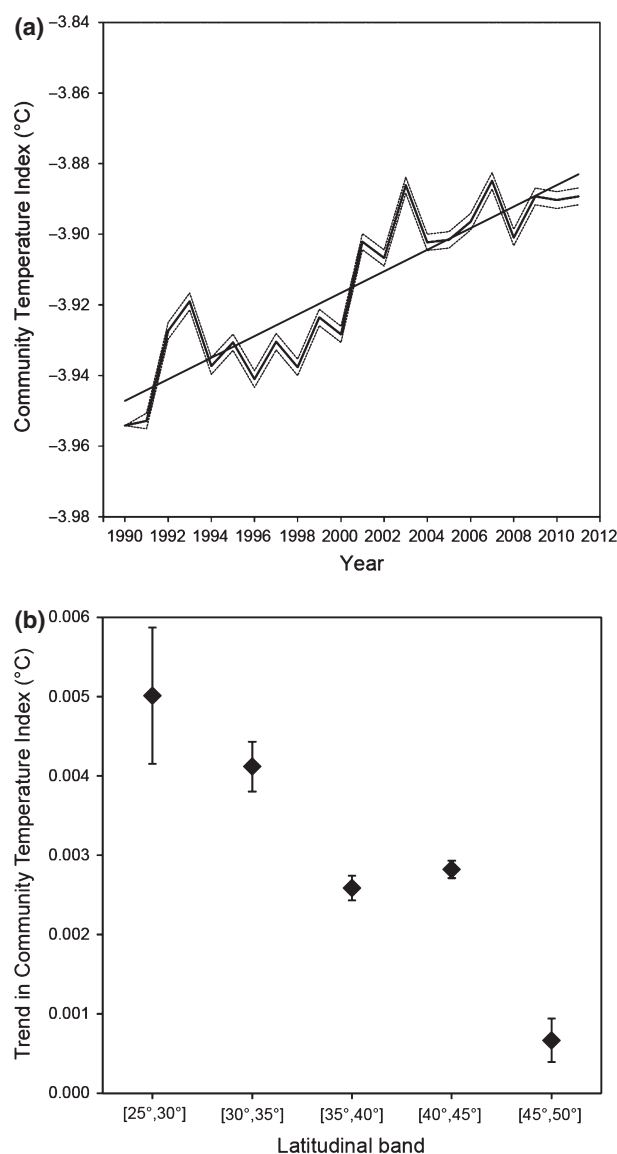


Fig. 3 (a) Increasing temporal trend of CTI across all Eastern North America from 1990 to 2011 (\pm SE of the mean in dashed lines) and (b) mean trends of CTI within 5-degree latitudinal bands for the same time period demonstrating stronger CTI changes in southerly latitudes. Mean trends over time and associated standard errors have been estimated using a GLMM.

ranked using AIC_c (Burnham & Anderson, 2002). The models with $\Delta AIC_c < 2$ were identified as models with the highest support, given the data. If multiple models had strong support, we calculated parameter estimates using model averaging and unconditional standard errors (Johnson & Omland, 2004). All analyses were performed using R version 3.0 (R Development Core Team, 2013) and GLMM were run using the R package nlme (Pinheiro *et al.*, 2007). Parameter estimates and associated standard errors are given as (mean estimates \pm SE).

Results

The CTI of wintering birds in eastern North America has increased steadily from 1990 to 2011 (Fig. 3a). We found positive trends using both CTI ($2.7 \pm 0.1 \times 10^{-3} \text{ }^\circ\text{C yr}^{-1}$, t -value = 32.92, $P < 0.001$; Fig. 3a) and weighted CTI ($1.9 \pm 0.1 \times 10^{-3} \text{ }^\circ\text{C yr}^{-1}$, t -value = 18.52, $P < 0.001$). The trend estimate of increasing CTI was higher than the trend from weighted CTI, suggesting that larger changes in CTI can be captured using occurrence only data. On the basis of the ratio between the temporal trend (see above) and the spatial gradient ($-3.8 \pm 0.02 \times 10^{-4} \text{ }^\circ\text{C km}^{-1}$) of the CTI, we found a northward shift in the community composition of wintering birds of about 7.01 km (± 0.24) per year, resulting in a total shift of 155 (± 5) km between 1990 and 2011. Using the weighted CTI, we also documented a comparable northward shift in CTI (146 ± 10 km). Along the latitudinal gradient, we found stronger CTI trends in more southerly latitudes (Fig. 3b), and these results were similar for both CTI and weighted CTI. We found no significant bias in CTI trends that could result from a geographic shift in

sampling across the years (Tables S3 and S4 in Data S3, Figures S4 and S5 in Data S3).

Changes in CTI across eastern North America were best explained by accounting for changes in winter minimum temperature (Table 1). For CTI, the global model was competitive and had strong support ($\omega_i = 0.33$) (Table 1). However, the model with temperature anomalies calculated over 5 and 35 years had the overall strongest support ($\omega_i = 0.67$). Over long-term (35-year time lag), increases in CTI were associated with warming trends in minimum winter temperature ($\beta = 0.106 \pm 0.003$). Over shorter time lags (5 years); however, increases in CTI changes were more likely in regions experiencing cooling winter temperatures (5 years: $\beta = -0.011 \pm 0.001$). Using the weighted CTI, the global model (including all time lags) had the strongest support ($\omega_i = 1.0$) (Table 1). We found that parameter estimates from this model were similar to the results for CTI.

All 38 species contributed positively toward the temporal trend of the CTI (Table 2). Across eastern North America, Carolina Wren (*Thryothorus ludovicianus*) ($C_{sp} = 38.68\%$), Eastern Bluebird (*Sialia sialis*) ($C_{sp} = 22.90\%$), Red-bellied Woodpecker (*Melanerpes carolinus*) ($C_{sp} = 19.95\%$), Purple Finch (*Carpodacus purpureus*) ($C_{sp} = 19.83\%$) and Accipiter *sp* ($C_{sp} = 18.98\%$) are the top five species that contributed most toward the overall CTI trend (Table 2). When using the weighted CTI, 35 of the 38 species contributed positively toward the temporal trend. Specifically, smaller-bodied species such as American Tree Sparrow (*Spizella arborea*) and Chipping Sparrow (*Spizella passerine*) were more influential using the weighted CTI.

Table 1 GLMM results examining effects of average minimum temperature (anomalies) on CTI and weighted CTI. Explanatory variables include anomalies in winter minimum temperature ($^\circ\text{C}$) calculated at time windows of 1 (Lag1 year), 5 (Lag5 years), and 35 (Lag35 years) years. We report the number of model parameters (k), sample-size adjusted Akaike Information Criterion (AIC_c), delta AIC_c (ΔAIC_c), and model weights (ω_i). All models included Year and Effort as fixed effects, random slopes and intercepts, and a first order autoregressive covariance. For both CTI and weighted CTI, we found strong support that minimum temperatures were influencing changes in CTI across eastern North America. Best-fitting models with $\Delta AIC_c < 2$ are in bold

Model	CTI				Weighted CTI			
	k	AIC_c	ΔAIC_c	ω_i	k	AIC_c	ΔAIC_c	ω_i
Lag1 year	9	-131951	1015.4	0.00	9	-113188	550.2	0.00
Lag5 years	9	-131974	992.6	0.00	9	-113244	494.0	0.00
Lag35 years	9	-132715	252.0	0.00	9	-113482	256.0	0.00
Lag1 year + Lag5 years	10	-132032	935.1	0.00	10	-113243	495.6	0.00
Lag1 year + Lag35 years	10	-132746	220.7	0.00	10	-113601	137.6	0.00
Lag5 years + Lag35 years	10	-132967	0.0	0.67	10	-113713	25.1	0.00
Lag1 year + Lag5 years + Lag35 years	11	-132965	1.4	0.33	11	-113738	0.0	1.00
Null model	8	-131938	1028.9	0.00	8	-113168	570.0	0.00

Table 2 Results from the jackknife analyses for CTI and weighted CTI. C_{sp} is the difference (%) between the Year coefficients estimated using the global and those from the jackknife models excluding the named species. A positive value indicates that the species contributed toward the CTI trend. Most influential species ($C_{sp} > 10\%$) on CTI trend and/or weighted CTI trend are in bold

Common name	Scientific name	C_{sp} (CTI)	C_{sp} (weighted CTI)
Accipiter sp.	Accipiter sp.	18.98	13.54
American Crow	<i>Corvus brachyrhynchos</i>	9.87	7.79
American Goldfinch	<i>Spinus tristis</i>	6.37	6.23
American Robin	Turdus migratorius	12.28	10.99
American Tree Sparrow	Spizella arborea	14.08	23.94
Blue Jay	<i>Cyanocitta cristata</i>	3.42	2.60
Brown Creeper	<i>Molothrus ater</i>	9.12	9.78
Brown-headed Cowbird	Certhia americana	10.97	6.21
Carolina Wren	Thryothorus ludovicianus	38.68	28.32
Cedar Waxwing	Bombycilla cedrorum	12.11	11.45
Chickadee sp.	<i>Poecile sp.</i>	8.76	6.76
Chipping Sparrow	Spizella passerine	13.58	23.62
Common Grackle	Quiscalus quiscula	10.63	9.24
Dark-eyed Junco	Junco hyemalis	16.45	-13.34
Downy Woodpecker	<i>Picoides pubescens</i>	4.50	6.98
Eastern Bluebird	Sialia sialis	22.90	24.12
European Starling	<i>Sturnus vulgaris</i>	4.81	1.09
Fox Sparrow	Passerella iliaca	12.41	10.63
Hairy Woodpecker	<i>Picoides villosus</i>	3.97	6.08
House Sparrow	<i>Passer domesticus</i>	3.72	-16.34
Mourning Dove	<i>Zenaidura macroura</i>	4.64	-1.80
Northern Cardinal	<i>Cardinalis cardinalis</i>	5.12	9.79
Northern Flicker	Colaptes auratus	11.16	9.98
Northern Mockingbird	Mimus polyglottos	7.25	10.08
Pileated Woodpecker	Dryocopus pileatus	12.40	10.43
Purple Finch	Carpodacus purpureus	19.83	32.28
Red-bellied Woodpecker	Melanerpes carolinus	19.95	15.67
Red-tailed Hawk	Buteo jamaicensis	14.26	11.41
Red-winged Blackbird	Agelaius phoeniceus	11.31	9.61
Rock Pigeon	Columba livia	13.63	13.34
Song Sparrow	<i>Melospiza melodia</i>	9.60	9.74
Towhee sp.	Pipilo sp.	12.15	10.39
Tufted Titmouse	<i>Baeolophus bicolor</i>	4.33	4.24
White-breasted Nuthatch	<i>Sitta carolinensis</i>	3.59	2.42
White-crowned Sparrow	Zonotrichia leucophrys	13.59	13.06
White-throated Sparrow	<i>Zonotrichia albicollis</i>	9.65	7.52
Yellow-bellied Sapsucker	Sphyrapicus varius	17.42	12.71
Yellow-rumped Warbler	Dendroica coronata	18.39	15.10

Species contribution to CTI trend was influenced by body mass (BM), migratory strategy (MS), northern range boundary (NB) and trends in occupancy (Occ) (Table 3). We found that the models with strongest support ($\omega_i = 0.61$) included BM, MS, NB, Occ, and two-second-order interaction terms (BM : Occ and NB : Occ) (Table 3). Species driving the increase in CTI across eastern North America were generally temperate migrants ($\beta = 3.90 \pm 1.50$) and southerly distributed ($\beta = -2.04 \pm 0.72$). Smaller-bodied ($\beta = -0.29 \pm 0.75$) and increasing birds ($\beta = 1.70 \pm 0.88$) also contributed positively toward CTI trends, but both these estimates

had 95% confidence intervals that included 0 (Fig. 4a). There was a strong, positive interaction of body mass and changes in occupancy (BM : Occ, $\beta = 2.66 \pm 1.02$, Fig. 4a). We found similar results after accounting for phylogenetic relatedness (MS, $\beta = 3.96 \pm 1.51$; NB, $\beta = -1.97 \pm 0.74$; BM, $\beta = -0.29 \pm 0.75$; Occ, $\beta = 1.85 \pm 0.93$; BM : Occ, $\beta = 2.65 \pm 1.02$). When considering only the most influential species ($C_{sp} > 10\%$), we found similar results except that the models with strongest support did not include MS (Fig. 4a). The *ad hoc* analysis with the phylogenetic correction resulted in a single best-fitting models including only NB, Occ

Table 3 Results from the top five GLM models testing the influence of species contribution ($C_{sp} > 0$) on CTI and weighted CTI trends. We report the number of model parameters (k), sample-size adjusted Akaike Information Criterion (AIC_c), delta AIC_c (ΔAIC_c), and model weight (ω_i). Predictor traits are body mass (BM), migratory strategy (MS), northern range boundary (NB), and trends in occupancy (Occ). Models with strongest support are in bold ($\Delta AIC_c > 2$)

Model	k	AIC_c	ΔAIC_c	ω_i
$C_{sp} > 0$ (CTI)				
BM + MS + NB + Occ + BM :	8	217.3	0.0	0.31
Occ + NB : Occ				
BM + MS + NB + Occ + BM :	7	218.6	1.3	0.16
Occ				
MS + NB + Occ	5	218.8	1.6	0.14
MS + NB + Occ + NB : Occ	6	219.6	2.4	0.09
BM + MS + NB + Occ + BM :	9	220.8	3.5	0.05
NB + BM : Occ + NB : Occ				
$C_{sp} > 0$ (weighted CTI)				
NB + Occ + NB : Occ	5	204.8	0.0	0.34
MS + NB + Occ + NB : Occ	6	206	1.2	0.19
NB + Occ	4	207.3	2.4	0.10
BM + NB + Occ + NB : Occ	6	207.8	2.9	0.08
BM + NB + Occ + BM : Occ +	7	208.9	4.0	0.05
NB : Occ				

and the corresponding interaction (NB : Occ), but the parameter estimates were quantitatively similar to those without the correction. Using weighted CTI for all species, the models with strongest support included MS, NB, and Occ, and the interaction between these two last variables (NB : Occ) (Table 3). The model-averaged coefficients for these predictors were comparable to those estimated using CTI (Fig. 4b). While the phylogenetic analysis resulted in a single best-fitting model including BM instead of MS, the parameter estimates were similar. Results differed slightly when considering only the most influential species ($C_{sp} > 10\%$), with a single best-fitting model showing a strong effect of smaller-bodied species ($\beta = -2.425 \pm 1.02$). MS was not included in the model and the northern boundary effect was weaker ($\beta = -1.22 \pm 1.39$) (Fig. 4b). Full model selection results are given in Tables S5 and S6 in Data S4, and results with the phylogenetic correction are provided in Tables S7 and S8 in Data S7.

The subset of the most influential species on CTI trends varied across latitudes (Table 4). Southerly distributed species, like the Chipping Sparrow and Yellow-rumped warbler (*Setophaga coronate*), contributed more to the CTI trend within the southernmost latitudinal bands. Others, like the Eastern Bluebird and Carolina Wren were the most influential at the northern limit of their range, 35–40°N and 40–45°N latitudes,

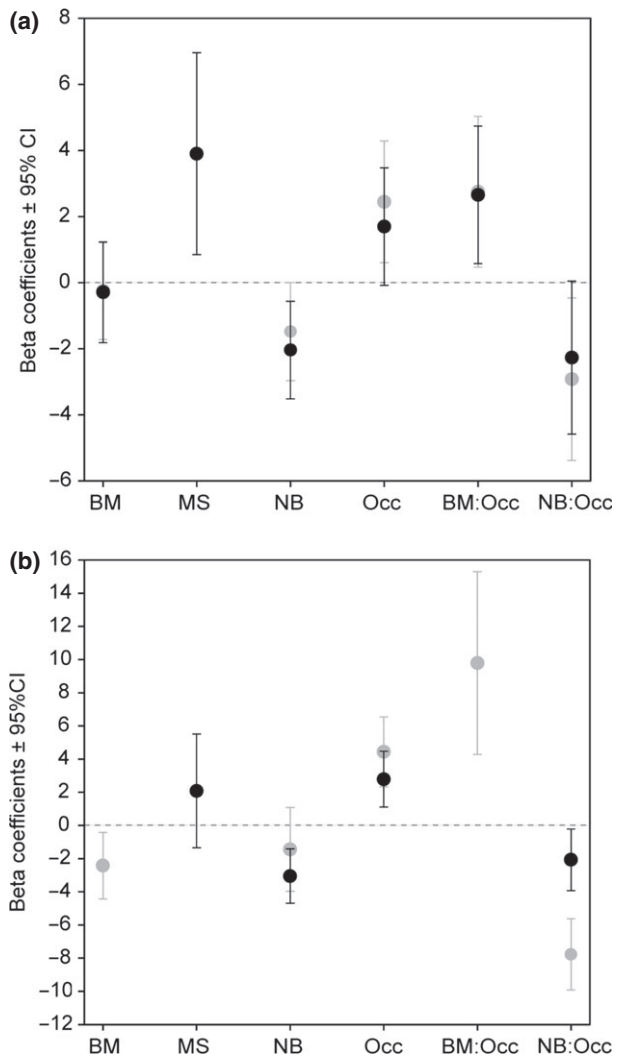


Fig. 4 Parameter estimates and 95% confidence interval for GLM models testing species contribution to (a) CTI trend and (b) weighted CTI trend, in relation to body mass (BM), migratory strategy (MS), northern boundary (NB) and occupancy (Occ), and relevant interactions. Dark dots correspond to all species that contributed toward the trends ($C_{sp} > 0$) and gray dots correspond to the most influential species ($C_{sp} > 10$). All parameter estimates are model-averaged beta coefficients if there was more than one competitive model. (a) Temperate migrants (significantly different from resident, considered as the control group) and southerly distributed species contributed most toward the CTI trend. Species increasing in occupancy, and especially southerly species increasing in occupancy, were the most influential on CTI trend. (b) Southerly distributed species and those increasing in occupancy most contributed toward the weighted CTI trend. The most influential species contributing toward positive CTI trends were smaller-bodied southerly species increasing in occupancy.

respectively. Within each latitudinal band, the top most influential species remained the same using the CTI or weighted CTI.

Table 4 Results from the jackknife analysis within 5-degrees latitudinal bands. We report the top five species that most contributed toward the CTI and weighted CTI trends and their respective C_{sp}

Latitudinal band	C_{sp} (CTI)	C_{sp} (weighted CTI)
(45–50°N)	Northern Mockingbird (67.53)	
	Purple Finch (67.2)	
	Rock Pigeon (62.63)	
	Accipiter sp. (59.39)	
	Mourning Dove (58.01)	
(40–45°N)	Carolina Wren (50.91)	Carolina Wren (57.07)
	Red-bellied Woodpecker (30.42)	Purple Finch (55.78)
	Accipiter sp. (24.93)	American Tree Sparrow (50.52)
	Eastern Bluebird (23.46)	Eastern Bluebird (36.26)
	Purple Finch (21.61)	Red-bellied Woodpecker (36.15)
(35–40°N)	Eastern Bluebird (23.56)	Purple Finch (24.76)
	Carolina Wren (22.69)	Eastern Bluebird (22.48)
	Yellow-rumped Warbler (16.71)	Carolina Wren (15.59)
	Chipping Sparrow (16.39)	Chipping Sparrow (13.36)
	Dark-eyed Junco (15.65)	Dark-eyed Junco (10.91)
(30–35°N)	Yellow-rumped Warbler (26.65)	Chipping Sparrow (41.47)
	Eastern Bluebird (19.19)	Purple Finch (14.31)
	Dark-eyed Junco (18.36)	Yellow-rumped Warbler (13.12)
	Purple Finch (17.75)	Dark-eyed Junco (12.76)
	Chipping Sparrow (16.91)	Eastern Bluebird (11.59)
(25–30°N)	Yellow-rumped Warbler (28.75)	Chipping Sparrow (62.13)
	Chipping Sparrow (26.59)	Yellow-rumped Warbler (9.29)
	Carolina Wren (25.14)	Carolina Wren (8.63)
	Northern Mockingbird (8.89)	Northern Mockingbird (7.26)
	House Sparrow (6.06)	Blue Jay (2.54)

There is no result for species contribution (C_{sp}) to weighted CTI within the northernmost latitudinal band (45–50°N) since there was no significant trend.

Discussion

We found compelling evidence that, over the span of 22 years, the winter bird communities of eastern North America became increasingly dominated by warm-adapted species. This pattern proved robust using two forms of a functional index, CTI, suggesting that community changes were not simply reflecting minor fluctuations in local abundance, but broader shifts in occurrence. This study represents the first use of CTI to capture changes in winter bird communities in North America. When compared to other regions in the world, the increasing CTI trend we found appears to be a broader phenomenon (Devictor *et al.*, 2008; Godet *et al.*, 2011; Lindström *et al.*, 2013). For instance, although the index was applied on different bird populations (i.e., European breeding birds), we found changes in CTI about the same magnitude of changes in Europe over 1990–2008 ($2.6 \times 10^{-3} \text{ } ^\circ\text{C yr}^{-1}$, Devictor *et al.*, 2012). The fingerprint of climate change often relies on documenting range boundary shifts for individual species; however, there is a growing interest in quantifying whether these climate-mediated changes

result in the reshuffling of biological communities (Tingley & Beissinger, 2013).

Climate is considered a critical environmental constraint shaping the broad-scale distribution and diversity of communities across geographic scales (Pearson & Dawson, 2003). At more local scales, habitat loss and fragmentation have a clear effect on bird abundance and occurrence, but land use changes only account for a small percentage of northward shifts among winter birds (La Sorte & Thompson, 2007). In a more recent study, Kampichler *et al.* (2012) have shown that the effects of climate and land use changes on bird communities seem to differ in speed and direction among habitats. The species included in this study are considered to be adapted to human-modified landscapes and take advantage of supplemental food resources. Many of these same species, however, have northern range limits that are primarily constrained by minimum temperature, although these bioclimatic relationships can be modified by urbanization (Zuckerberg *et al.*, 2011). We found that changing winter temperatures are promoting a shift to communities characterized by warm-adapted birds. In support of this pattern, CTI increases

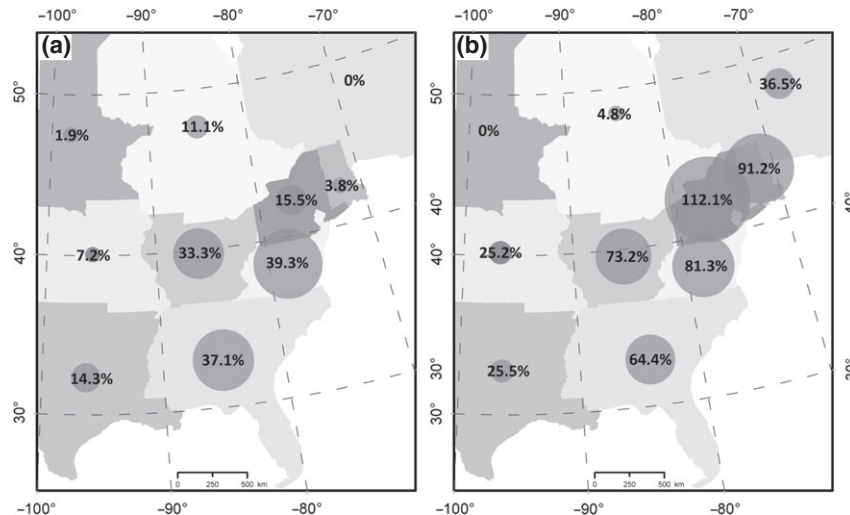


Fig. 5 Temporal trends in relative occupancy (frequency of site visitation) within FeederWatch regions throughout Eastern North America for (a) the Chipping Sparrow and (b) the Carolina Wren.

were closely associated with areas demonstrating long-term (>30 years) increases in winter minimum temperatures. It is likely that milder winters have benefited warm-adapted birds at geographic scales, but we also found that patterns of increasing CTI were associated with regions experiencing short-term (<5 years) cooling (Fig. 2). Similarly, La Sorte & Jetz (2012) found a delayed climate niche tracking for many North American winter birds that was attributed to a 'lull' in the continental warming trend. They suggested that the weakening in the warming trend provided an opportunity for species to accelerate their climate niche tracking. We found that increases in CTI were closely associated with the 'warming hole' in the southeastern region of the United States (Pan *et al.*, 2004; Kunkel *et al.*, 2006; Figure S6 in Data S6). This warming hole is thought to be the result of cold-air advection in winter and low-level moisture convergence in the summer (Meehl *et al.*, 2012). This warming hole might provide a critical window for individual species to 'catch up' to their respective climatic niches while temperatures in adjacent regions rise, ultimately resulting in a more rapid shift in community composition.

An increase in the prevalence of warm-adapted birds within a community, and a subsequent increase in CTI, could be achieved through multiple population-level pathways. CTI could increase as a result of poleward shifts of warm-adapted birds along their northerly range limits as they take advantage of milder winter conditions. Alternatively, CTI increases could result from cold-adapted birds becoming less common and retracting along their southern range boundary through local extirpation. Past studies have emphasized that the northerly 'cool-edge' range limits of temperate species

are more likely to be constrained by climatic factors than southerly 'warm-edge' range limits where biotic interactions are thought to dominate (MacArthur, 1984; Parmesan, 2006; La Sorte & Thompson, 2007; Jiguet *et al.*, 2010). Our prediction that CTI changes would be strongest in northerly latitudes and driven by range expanding southerly birds was generally not supported (Fig. 2b). We found that the stronger positive CTI trends in southerly latitudes were driven by warm-adapted birds increasing in their local abundance and regional occurrence. For example, we found that the Chipping Sparrow was a strong driver of CTI trends in southerly latitudes and in many of these regions has increased in occurrence from 30% to 40% at PFW sites between 1990 and 2011 (Fig. 5a) with a concurrent increase in abundance from 4 to 10 individuals per site on average. The Carolina Wren, another smaller bodied, southerly distributed species that strongly contributed to the CTI trend, exhibits the same patterns of increase in occupancy throughout the study area (Fig. 5b). Despite diminished trends in CTI in the more northerly latitudes, these trends were also driven by southerly species expanding their range (e.g., Carolina Wren and Eastern Bluebird) as opposed to cold-adapted birds becoming locally extirpated and shifting northward.

The predominance of southerly, warm-adapted birds driving changes in CTI through range expansion and increasing local abundance does not preclude the importance of range contractions or declines in abundance of northerly species. Few studies have focused on poleward shifts along more southerly 'warm-edge' range limits, but Zuckerberg *et al.* (2009b) found that many northerly species in New York State were shifting

northward in their range boundaries and that this rate was equal to or greater the shift of southerly species. More recently, a meta-analysis of 178 species found that the majority of species (108) had warm-edge range limits set at least partly by temperature (Cahill *et al.*, 2014). Climate change may push some populations closer to the centroid of their climatic niche and other populations farther away (Tingley *et al.*, 2009). Likewise, although broad CTI trends were similar using both forms of CTI, latitudinal differences in which species were most influential in driving CTI trends suggests that the species contributing to changes in community composition do so through differential population dynamics. Insofar as winter bird species display highly variable responses to climate change, the resultant communities being reassembled under climate change is likely to occur in a geographically non-uniform fashion (La Sorte & Jetz, 2012).

Smaller-bodied species contributed most to the CTI trend suggesting that these species might respond rapidly to climate change. Our results are in accordance with previous findings concerning the range dynamics of smaller-bodied winter bird species – such as northward shifts of Carolina Wren and Purple Finch (Niven *et al.*, 2009). A higher contribution of smaller, southerly distributed species to increasing CTI is consistent with Bergmann's rule that populations and species of larger size are found in colder environments and species of smaller size are found in warmer regions (Mayr, 1956). In our study, however, this biogeographic principle is supported for some, but not all, birds contributing toward the global trend of CTI. Previous studies have not always been in agreement with Bergman's rule (Millien *et al.*, 2006; La Sorte *et al.*, 2009), and there remains strong debate as to the underlying mechanism (Ashton *et al.*, 2000; Ashton, 2002). As an example, milder winter temperatures might facilitate the dispersal of larger-bodied individuals (Jenkins *et al.*, 2007) and the increased diversion of energy from maintenance to growth (Millien *et al.*, 2006). In support of the expectations based on Bergmann's rule, however, Van Buskirk *et al.* (2010) analyzed over four decades of banding station data and found widespread declines in body size that were related to warming regional temperatures. In our study, we found the effect of body size was most apparent in estimated trends using weighted CTI, and suggests the impact of smaller-bodied species on winter bird communities was a result of subtle changes in species' relative abundance, rather than broad-scale changes in species' occurrences.

Recent theoretical studies emphasizes that the ability of bird species to respond to a shifting climate is largely dependent on their evolved ability to adjust their behavior under novel environmental conditions (i.e.,

phenotypic plasticity) (Vedder *et al.*, 2013). Our study demonstrates that life history traits associated with geographic range and migratory behavior play an important role in which species are more likely to respond to a warming winter. We found evidence of a higher contribution of temperate migrant species to the increasing CTI trend. This supports the hypothesis that migrants should be more adept at responding to changing environmental and climatic conditions than residents due to stronger dispersal abilities (Parmesan *et al.*, 1999). Most of the migrants in this study are considered facultative short-distance migrants for which phenological adaptations are more plastic compared to long-distance migrants (Both *et al.*, 2010). Nevertheless, the higher contribution of temperate migrants was not a strong signal, since it was not found among the most influential species on CTI trend. This can partly be explained because resident birds are also expected to benefit from winter warming (Rodenhouse *et al.*, 2009) as the abundance and demographics of these species is commonly thought to be limited by winter conditions (Brittingham & Temple, 1988; Newton 1998).

Climate change should not be viewed as the sole driver of changes in winter bird communities in eastern North America. Our study provides insights into the changing composition of winter bird communities, but it would be useful to explore other environmental changes such as shifting land use practices (Zuckerberg *et al.*, 2011; Barnagaud *et al.*, 2013). Birds are highly vagile and capable of dynamic changes in abundances that can respond to other factors such as shifting food resources (Kissling *et al.*, 2010). A potential cause of shifting winter bird distributions is that simply more people are engaged in feeding wild birds; however, recent national surveys do not support this trend. Although the number of participants in project Feeder-Watch has increased during the study period, the number of people who engage in feeding wild birds in their backyards has remained remarkably constant since the early 1990s. National surveys of wildlife-associated recreation in the United States have documented that an estimated 53 million people feed wild birds around their home and that this number has either decreased or remain relatively unchanged between 1991 and 2011 (U.S. Fish & Wildlife Service, 2011). In addition, any moderate increase in feeding would tend to favor any of these study species as all are frequent users of supplemental food. Biotic interactions may also be important when analyzing community shifts (Pearce-Higgins *et al.*, 2010). For example, recent population declines have been documented for Purple Finches (Wootton, 1996) and House Sparrows (Cooper *et al.*, 2007), and negative interactions with invasive House Finches (introduced in the 1940s) have been suggested as a

likely cause of these declines through competitive exclusion (Wootton, 1987; Cooper *et al.*, 2007). Given these findings, there remains a strong possibility that climate change could lead to shifting communities by either strengthening or weakening biotic interactions within winter bird communities (Post, 2013).

Tracing the fingerprint of climate change has focused primarily on distributional and phenological changes for individual species, but less is known on whether these species-specific responses are resulting in community-wide changes. Winter birds represent both a critical ecological indicator, and as backyard denizens, a potent tool for climate change communication. Herein, we documented a long-term and geographic increase in the prevalence of warm-adapted winter birds across eastern North America driven by smaller-bodied, migratory species who are increasing in their local abundance and regional occurrence. Interestingly, we found that this pattern is generally associated with long-term warming trends, but the presence of recent warming holes may serve as windows of high community turnover. It should be noted, however, that those windows will close in the future as warming holes are predicted to disappear with increasing surface temperatures (Meehl *et al.*, 2012). It appears that the well-documented pattern of northward shifting species is resulting in the broad-scale reshuffling of winter bird communities in North America.

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Supporting Information

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

- Data S1.** Supporting information on Species Temperature Index (STI).
- Data S2.** Description of wintering bird species traits
- Data S3.** Results of the randomization procedure
- Data S4.** Analysis of the influence of species traits on C_{sp} – without phylogenetic relatedness (GLM)
- Data S5.** Analysis of the influence of species traits on C_{sp} – with phylogenetic relatedness (GLMM)
- Data S6.** Averaged minimum winter temperature anomalies from 1990 to 2011 per latitudinal band.