

POLEWARD SHIFTS IN WINTER RANGES OF NORTH AMERICAN BIRDS

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Abstract. Climate change is thought to promote the poleward movement of geographic ranges; however, the spatial dynamics, mechanisms, and regional anthropogenic drivers associated with these trends have not been fully explored. We estimated changes in latitude of northern range boundaries, center of occurrence, and center of abundance for 254 species of winter avifauna in North America from 1975 to 2004. After accounting for the effect of range size and the location of the northern boundary, positive latitudinal trends were evident for the northern boundary (1.48 km/yr), center of occurrence (0.45 km/yr), and center of abundance (1.03 km/yr). The northern boundary, when examined across individual species, had the most variable trends (SD = 7.46 km/yr) relative to the center of occurrence (SD = 2.36 km/yr) and center of abundance (SD = 5.57 km/yr). Trends did not differ based on migratory status, but there was evidence that trends differed for species with ranges centered in the southern vs. northern portion of the study area. Species occurred more sporadically over time at northern range boundaries, and northern boundaries were associated with a concentration of colonization and extirpation events, with a greater prevalence of colonization events likely promoting poleward trends. Regional anthropogenic drivers explained ~8% of the trend for the northern boundary, 14% for the center of occurrence, and 18% for the center of abundance; however, these effects were localized in the northern portion of species' ranges and were associated with distributional changes within ranges, primarily abundance, producing patterns that mimicked poleward movements. We conclude that poleward distributional shifts represent the interaction between climate change and regional factors whose outcome is determined by the scale of the analysis and the biotic and abiotic features in the region, and how anthropogenic activities have impacted these features.

Key words: abundance; Christmas Bird Count; common species; distribution of avifauna; geographical range; global climate change; North America; temporal turnover; winter range.

INTRODUCTION

Modern global climate change (Karl and Trenberth 2003) is thought to promote broad-scale alterations in ecological systems and evolutionary processes (Hughes 2000, McCarty 2001, Walther et al. 2002, Davis et al. 2005, Root et al. 2005, Parmesan 2006), including the poleward or positive latitudinal shift in geographic ranges, which has been documented for a variety of taxonomic groups (Parmesan and Yohe 2003, Root et al. 2003, Hickling et al. 2006). However, range boundaries define the limits of a species' biotic and abiotic requirements and represent a complex and poorly understood ecological phenomenon (reviewed in Brown et al. 1996, Gaston 2003). Moreover, it has been argued that relying exclusively on range boundaries to predict or model the response of taxa to climate change will lead to partial or misleading conclusions (Davis et al. 1998a, b, Hill et al. 2001, Warren et al. 2001, Honnay et al. 2002, Davis et al. 2005, Shoo et al. 2005, 2006). In fact, few investigations actually focus on

complete range boundaries; instead, the majority of investigations infer range shifts from changes in partial range boundaries or changes in species composition in local communities (Parmesan 2005). These shortcomings are particularly relevant when attempting to make inference to the effect of climate change when local and regional anthropogenic drivers often provide more parsimonious explanations (e.g., habitat modification or land-use change). Therefore, shifts in range boundaries, even complete range boundaries, would appear to represent a limited biological measure of the impact of climate change on geographic ranges in particular and ecological systems in general.

Our first goal in this study is to examine recent latitudinal trends in geographic ranges to assess the relationship between patterns occurring on northern boundaries and patterns occurring within the interior of the range. To test the hypothesis that climate change has promoted broad-scale latitudinal trends, we will test several predictions. First, positive latitudinal trends should be evident for northern boundaries, and these patterns should be paralleled by similar trends occurring within the interior of the range. Second, positive latitudinal trends should be stronger for species whose ranges are centered in the northern vs. southern portion

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of the study area because abiotic factors are thought to limit distributions at higher latitudes (Brown et al. 1996) and higher latitudes are thought to be experiencing more substantial warming trends (Parmesan et al. 1999). Finally, we predict that changes in latitude should be greater for migrants than for residents because, based on theory and evidence, species with stronger dispersal abilities should be more adept at responding to changing environmental and climatic conditions (Parmesan et al. 1999).

Our investigation examined latitudinal trends for species in avian assemblages wintering in North America over a 30-year time period. We focused on avian distributions because birds are thought to respond more readily to climate change (Araújo and Pearson 2005), and birds have been the subject of the majority of studies searching for evidence of poleward shifts (Root 1994, Thomas and Lennon 1999, Valiela and Bowen 2003, Brommer 2004, Hickling et al. 2006). However, these investigations were conducted in small geographic regions using relatively few species. In contrast, our investigation will provide a comprehensive assessment of latitudinal trends by examining changes in complete northern boundaries and changes in occurrence and abundance within the range for a wide selection of species across the longitudinal extent of North America.

Our second goal is to explore the ecological mechanisms responsible for observed trends. Much attention has focused on using evidence of range shifts to identify biotic and abiotic factors that delineate species' range boundaries (Parmesan et al. 2005). However, the structure of the underlying ecological mechanisms that actually promote range shifts have not been fully explored, specifically, the nonuniform distributions of temporal turnover events (i.e., extirpation and colonization events) on northern and southern range boundaries (Parmesan et al. 1999). We examined the structure of these mechanisms based on an analysis of temporal turnover dynamics occurring within geographic ranges, using methods developed in an earlier investigation (La Sorte and Boecklen 2005).

Our third goal is to examine the influence of regional anthropogenic drivers in any observed distributional trends. We used the methods cited above (La Sorte and Boecklen 2005) to identify species that experienced extreme colonization or extirpation events. These extreme events indicate the presence of substantial distributional changes, changes likely driven by intensive regional anthropogenic drivers, and not weaker and more uniform global drivers such as climate change. This conclusion is supported by evidence that regional anthropogenic factors promoted extreme colonization events for several species of breeding avifauna in North America (La Sorte and Boecklen 2005). Addressing this goal will determine the extent to which regional factors are promoting or interfering with broad-scale distributional trends driven by climate change.

METHODS

Data source and selection

We used data from the North American Christmas Bird Count (CBC; National Audubon Society) from 1975 to 2004 for the analysis (Bock and Root 1981). We chose 1975 as a starting date because observer effort at CBC circles became relatively consistent at approximately this time. CBC surveys are conducted within 12 km radius circles for a period of one day during a two-week period centered approximately on 25 December. From 3387 CBC circles, 856 were selected for analysis that were sampled at least once during each of 10 three-year time periods (i.e., 1975–1977, 1978–1980, ..., 1999–2001, 2002–2004). The 856 circles sampled locations in the United States, Canada, and northern Mexico, with the greatest concentration located in the northeastern United States (Fig. 1). Thus, we sampled locations in the south-central portion of the north temperate zone (i.e., from ~30–50° north latitude; Fig. 1).

We selected 254 avian species for analysis based on the following criteria. We merged all subspecies and races into single species and merged species that were split during the time of the survey. We excluded species that were identified as accidental or had winter ranges outside of the study area, were associated primarily with marine environments, or were exclusively nocturnal. We then selected species that contained either their entire winter range within the study area or whose northern boundary was located in the study area determined using distributional maps from a variety of sources (e.g., Kaufman 1996, Poole 2005). We also used these sources to identify whether each of the 254 species was migratory ($n = 184$) or nonmigratory ($n = 70$) within the study area, based on the relative location of winter and breeding ranges. Finally, we removed species that occurred at <10 circles or were not observed every year during the survey period (see Appendix for identities and migratory status for all 254 species).

Analysis of latitudinal trends

We examined latitudinal trends for three components of the geographic range: (1) northern boundary, (2) center of occurrence, and (3) center of abundance. We estimated these components for each of the 254 species for each year of the survey. The northern boundary was calculated as the maximum latitude of the CBC circle where a species was documented. The center of occurrence was calculated as the mean latitude of CBC circles where a species was documented. The center of abundance was calculated as

$$y_{cm} = \frac{\sum_{i=1}^n m_i y_i}{\sum_{i=1}^n m_i}$$

where y_{cm} is the latitude of the center of mass for a

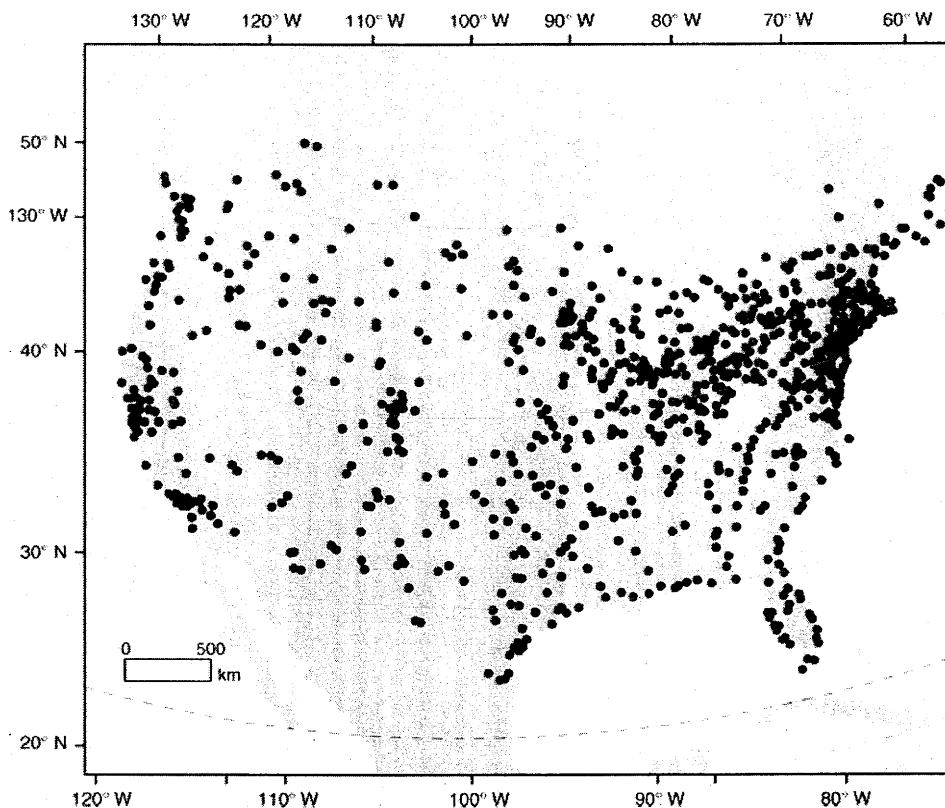


FIG. 1. Location of 856 North American Christmas Bird Count circles considered in the analysis plotted on a 10° interval grid of north latitude and west longitude. The dashed line is the Tropic of Cancer at 23.5° north latitude, and the map projection is Lambert Azimuthal Equal Area.

collection of n CBC circles with masses $m_1, m_2, \dots, m_n$ and latitudes $y_1, y_2, \dots, y_n$, where mass is defined as the total number of individuals observed at a CBC circle divided by the total number of party hours. Our estimate of mass, therefore, was based on the number of individuals documented per hour of survey effort.

We examined latitudinal changes in the three geographic range components using three separate linear-mixed models. We included year as a fixed effect and treated species as a random effect in all three models. The first model included latitude of the northern boundary as the response, with the annual number of CBC circles where the species was observed as a fixed effect. The second model included latitude of the center of occurrence as the response, with annual number of CBC circles where the species was observed and annual maximum latitude as fixed effects. The third model included latitude of the center of abundance as the response, with annual number of CBC circles where the species was observed and annual maximum latitude as fixed effects.

These methods allowed us to explicitly model trends for individual species and account for between- and within-species variation in these trends. More specifically, these methods allowed us to account for variability in species-specific effects, in this case, variability in the

baseline level of the response and variability in the rate of change in the response over time across species. These methods also allowed us to control for effects that were shared across species, in this case, the association between the response and changes in range size and the northern boundary over time. To estimate latitudinal trends for individual species, we ran the same linear models described above for each species separately without the random effect.

We used migratory status for each species as a covariate in the linear-mixed models defined above to test if the latitudinal trends differed by migratory status. We also divided species into two groups whose winter ranges were centered either in the northern or southern portion of the study area. We used 36° north latitude as the demarcation and species' average latitude in 1975 to classify species into the northern and southern categories. (The median latitude for 1975 was 36°; thus each category had 127 species [see Appendix for species' classifications].) We included this category as a covariate in the linear-mixed models defined above to test if the latitudinal trends differed for northern vs. southern species. The linear-mixed model analysis was implemented using the library nlme and the function lme developed by Pinheiro and Bates (2000) and implement-

ed in R, version 2.3.0 (R Development Core Team 2006).

Analysis of temporal turnover

We analyzed patterns of temporal turnover of species at CBC circles from 1975 to 2004 using a modification of methods developed by La Sorte and Boecklen (2005). We classified each species at each CBC circle where it was observed into four categories: (1) Common if the species was observed nearly continuously during the time of the survey; (2) Colonized if the species colonized the circle during the time of the survey and was then observed nearly continuously; (3) Extirpated if the species was observed nearly continuously and then not observed at all; and (4) Not Common if a species did not fall into any of these three categories. We used binary presence/absence vectors (vectors consisting of two elements {0, 1}) to classify species. We measured the Euclidian distance from observed presence/absence vectors to ideal vectors that represented the expected pattern for the categories Common, Colonized, and Extirpated. Specifically, for a CBC circle that was surveyed for n years, a vector of length n that contained all 1's represented the expected pattern for Common species, the vector $[0, 0, \dots, 0, 1, 1, \dots, 1]$ represented the expected pattern for Colonized species, and the vector $[1, 1, \dots, 1, 0, 0, \dots, 0]$ represented the expected pattern for Extirpated species. For CBC circles that were sampled an even number of years, the expected vectors for the categories Colonized and Extirpated contained an equal number of 0's and 1's. For CBC circles that were sampled an odd number of years, the number of 0's was one less than the number of 1's. Therefore, this approach captured colonization and extirpation events that occurred at or near the halfway point of the survey and missed events that occurred early or late during the survey. As a consequence, this approach was able to document colonization and extirpation events more accurately by focusing on events that had the greatest likelihood of being actual turnover events (La Sorte and Boecklen 2005).

We used a modification of the resampling method described by La Sorte and Boecklen (2005) to calculate the probability that the Euclidean distances between the observed and idealized vectors occurred by chance alone. For a CBC circle that was observed n years, we generated 9999 random binary vectors containing a sequence of n Bernoulli trials where the probability of success (1) or failure (0) were equivalent (i.e., $P\{X=1\} = 0.5$ for each Bernoulli trial). Thus, each random vector contained an n -tuple of zeros and ones, and the collection of random vectors sampled the vertices in an n -dimensional hypercube where each vertex had an equal probability of occurring. The Euclidian distance from the expected vector to these random vectors was measured and where the observed distance occurred in this distribution allowed us to generate a P value. We classified a species into the categories Common,

Colonized, or Extirpated based on which category had the smallest P value below 0.1. If none of the P values was below 0.1, the species was classified as Not Common. Compared to the original resampling approach, this procedure provided, particularly for vectors that were dominated by either ones or zeros, more precise P values.

For each of the 254 species, we summed the number of CBC circles from the 856 where the species was classified as Common, Colonized, Extirpated, or Not Common. We plotted the number of CBC circles where species were designated as Colonized or Extirpated in a bivariate scatter plot and identified species that had extreme values for the number of circles classified as Extirpated or Colonized (La Sorte and Boecklen 2005). We also averaged, for each species, the latitude and longitude of CBC circles where each species was classified in each of the four categories. We then averaged these values across species to estimate the average location within species' ranges for each of the four categories. We also estimated the composition of the four categories within each species' range by calculating the proportion of CBC circles where a species was designated in each of the four categories. We then averaged these values across species. Finally, to test for differences between category pairs based on latitude and proportion, we used t tests when the assumptions for parametric analysis were met, and the bootstrap- t method using the R function `yuenbt` developed by Wilcox (2005) with 9999 bootstrap samples when these assumptions were not met.

RESULTS

Latitudinal trends

For the 254 species of winter avifauna considered in the analysis, the latitude of northern range boundaries increased on average during the time of the survey after accounting for the effect of range size ($t_{7364} = 3.575$, $P = 0.0004$). For fixed values of range size, the maximum latitude moved north ~ 1.48 km/yr (95% CI: 0.66 to 2.26 km/yr) from 1975 to 2004. The latitude of the center of occurrence increased ($t_{7363} = 2.672$, $P = 0.0076$) and the center of abundance increased ($t_{7363} = 3.395$, $P = 0.0007$) on average during the time of the survey after accounting for the effect of range size and the location of the northern boundary. For fixed values of range size and northern boundary, the center of occurrence moved north ~ 0.45 km/yr (95% CI: 0.12 to 0.78 km/yr) and the center of abundance moved north ~ 1.03 km/yr (95% CI: 0.44 to 1.63 km/yr) from 1975 to 2004.

Trend estimates for maximum latitude, average latitude, and center of mass did not differ based on migratory status after accounting for the effect of range size and the location of the northern boundary ($P > 0.33$). For species with winter ranges centered in the northern vs. southern portion of the study area, there was limited evidence the northern boundary increased at a greater rate for species in the southern portion of the

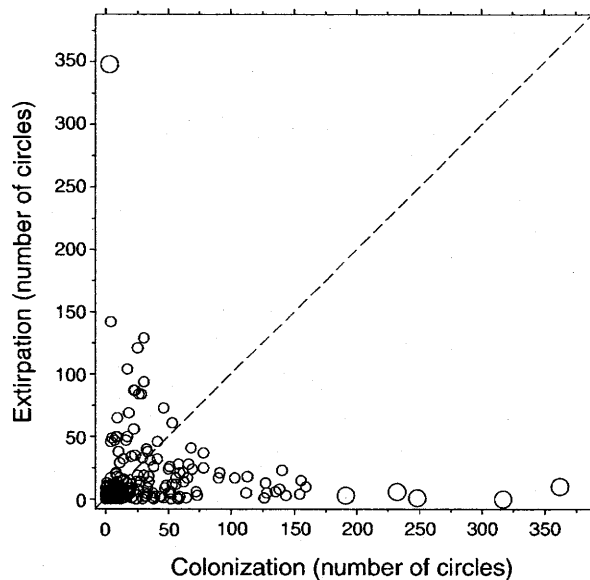


FIG. 2. Plot of the Christmas Bird Count (CBC) circles for the 254 species considered in the analysis: the number of circles where each species was designated as common and extirpated (Extirpation) vs. the number of circles where each species was designated as common and colonizing (colonization). These values were estimated from an analysis of temporal turnover dynamics for species observed at 856 CBC circles from 1975 to 2004 (see *Methods* for details on the analysis and description of categories). The dashed line is the line of perfect equality where the number of CBC circles colonized equals the number extirpated. The six large symbols represent outliers or species far from the line of equality that colonized many more CBC circles than they were extirpated from ($n = 5$) or were extirpated from many more CBC circles than they colonized ($n = 1$).

study area after accounting for the effect of range size ($t_{7363} = -1.667$, $P = 0.0956$); there was no evidence the center of occurrence increased at different rates after accounting for the effect of range size and the location of the northern boundary ($t_{7363} = -0.974$, $P = 0.3303$); and there was evidence the center of abundance increased at a greater rate for species located in the northern portion of the study area after accounting for the effect of range

size and the location of the northern boundary ($t_{7363} = 2.853$, $P = 0.0043$).

Based on the distribution of slope coefficients estimated individually for each of the 254 species, where positive coefficients indicated a northern advance in latitude and negative coefficients indicated a southern retreat, several patterns were evident (see Appendix for slope coefficients). Changes in the northern boundary showed the greatest variation across species after accounting for the effect of range size (range: -30.54 to 31.84 km/yr; $SD = 7.46$ km/yr). Changes in the center of abundance showed intermediate variation across species after accounting for the effect of range size and the location of the northern boundary (range: -13.82 to 39.34 km/yr; $SD = 5.57$ km/yr). Changes in the center of occurrence showed the least variation across species after accounting for the effect of range size and the location of the northern boundary (range: -7.63 to 20.35 km/yr; $SD = 2.36$ km/yr).

Turnover dynamics

Based on a bivariate plot of the number of CBC circles where each species was designated as Colonized by the number of CBC circles where each species was designated as Extirpated, several outliers were detected that contained extreme values (Fig. 2). The majority of species were clustered about the origin and the line of perfect equality, with evidence that five species had colonized many more CBC circles than they were extirpated from, and evidence that one species had been extirpated from many more CBC circles than they had colonized (Table 1; see the Appendix for the outcome of the turnover analysis for all 254 species).

If we examine at which CBC circles the five colonizing species were located (Fig. 3a), and at which CBC circles the one extirpated species was located (Fig. 3b), several patterns were evident. The five colonizing species were found primarily in the Upper Midwest and northeastern United States, but not exclusively. The single extirpated species occurred more exclusively in these regions. Overall, the majority of CBC circles where these

TABLE 1. The five species identified as experiencing extreme colonization events and the one species identified as experiencing an extreme extirpation event, with the number of Christmas Bird Count (CBC) circles where the species was identified as common (COM), common and extirpated (EXT), common and colonizing (COL), and present but not identified in any of the three common categories (NCOM).

Common name	Scientific name	COM	EXT	COL	NCOM
Colonized					
Wild Turkey	<i>Meleagris gallopavo</i>	85	10	362	197
House Finch	<i>Carpodacus mexicanus</i>	448	0	317	49
Bald Eagle	<i>Haliaeetus leucocephalus</i>	267	1	248	270
Hooded Merganser	<i>Lophodytes cucullatus</i>	288	6	232	257
Cooper's Hawk	<i>Accipiter cooperii</i>	464	3	191	164
Extirpated					
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	128	348	3	244

Notes: These values were estimated from an analysis of temporal turnover dynamics for 254 species documented at 856 CBC circles from 1975 to 2004. (See *Methods* for details on the analysis and description of categories.)

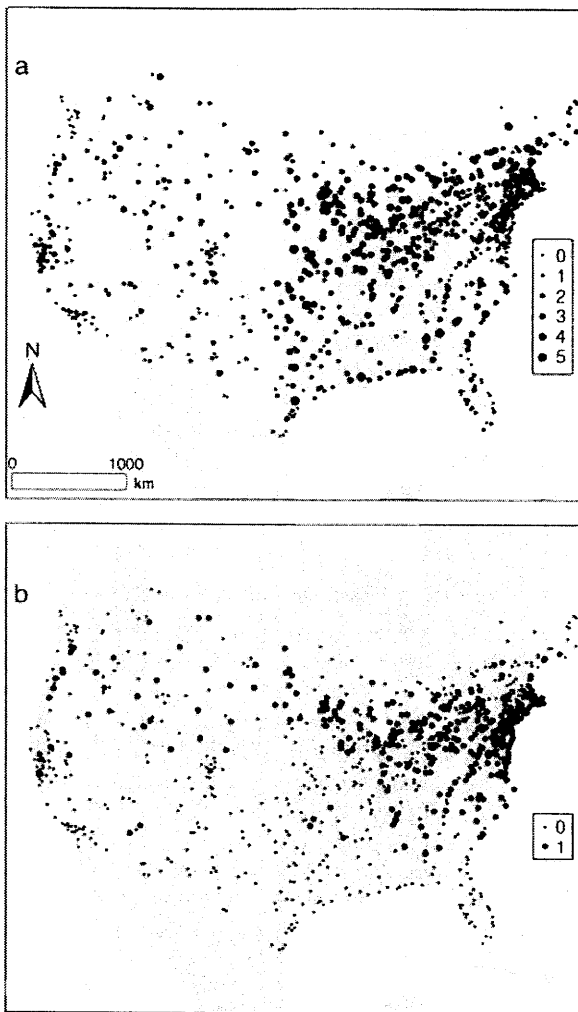


FIG. 3. The location of the 856 Christmas Bird Count (CBC) circles in North America with (a) the number of the five colonizing species found at each CBC circle represented by incrementally larger circles on a scale from 0 to 5 species, and (b) the presence or absence (1 or 0, respectively) of the one extirpated species at each CBC circle (see *Methods* for details on the analysis and description of categories). The map projection is Lambert Azimuthal Equal Area.

colonization and extirpation events occurred were located in the northern portion of the study area (Fig. 3).

Based on the bootstrap-*t* method, the proportion of circles where species were designated as Not Common exceeded the proportion designated as Common ($t = 5.750$, $P = 0.003$), and the proportion of circles where species were designated as Colonized exceeded the proportion designated as Extirpated ($t = 6.909$, $P \leq 0.001$). The average latitude within each species' range where the species was designated in the four categories differed on average (one-way ANOVA, $F_{3,965} = 17.919$, $P \leq 0.0001$; Fig. 4A). Based on *t* tests of category pairs, several patterns were evident (Table 2; Fig. 4A). On average, CBC circles where species were identified as Not Common were located the farthest north, while

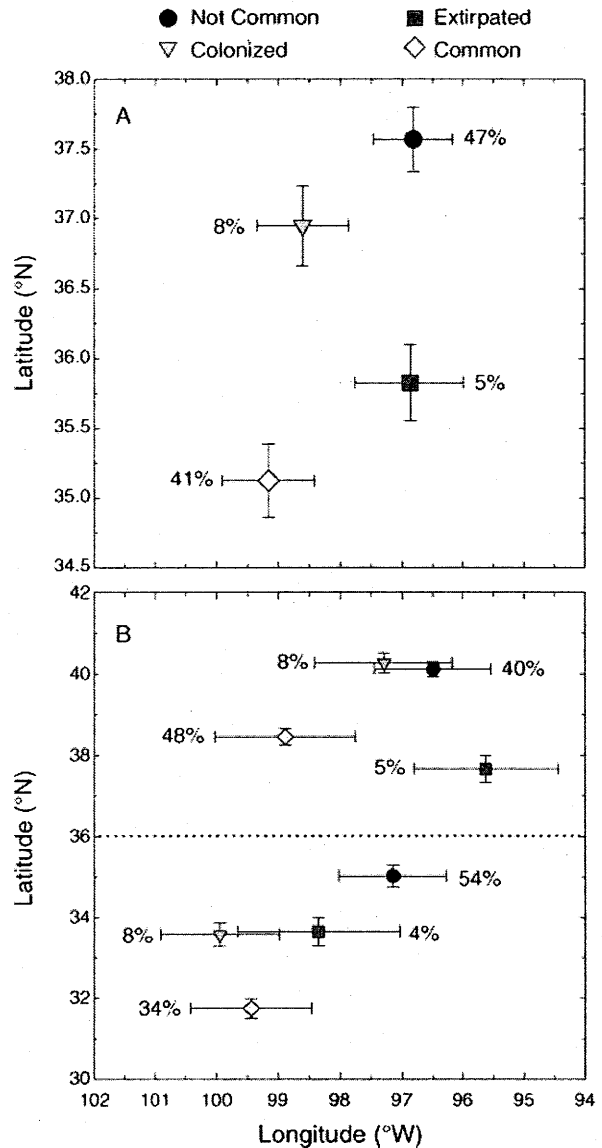


FIG. 4. Plot of latitude and longitude (mean $\pm$ SE) of Christmas Bird Count (CBC) circles in North America where species were identified in each of four categories based on an analysis of temporal turnover dynamics (see *Methods* for details on the analysis and description of categories). A total of 254 species documented at 856 CBC circles from 1975 to 2004 were considered in the analysis. Average locations are presented for (A) all 254 species considered in the analysis, and (B) 127 species located in the northern portion of the study area and 127 species located in the southern portion of the study area, based on average latitude in 1975, using 36° north latitude as the demarcation (dotted line). Latitude and longitude for each category were averaged for each species and then averaged across species within each category. Each category is also labeled by the percentage of CBC circles identified in each category averaged across species.

CBC circles where the species was identified as Common were located the farthest south. Colonization and Extirpation events were located, on average, between these two categories, with Colonization events occurring

TABLE 2. Pairwise comparisons (with no adjustments for multiple testing) of average latitude of Christmas Bird Count (CBC) circles in North America for species identified in four categories (see *Methods*) based on an analysis of temporal turnover dynamics.

Comparison	<i>t</i>	df	<i>P</i>
All species (<i>n</i> = 254)			
COM vs. COL	-4.952	965	≤0.0001
EXT vs. COL	-2.950	965	0.0033
EXT vs. COM	1.858	965	0.0635
NCOM vs. COL	1.678	965	0.0937
NCOM vs. COM	6.708	965	≤0.0001
NCOM vs. EXT	4.622	965	≤0.0001
Northern species (<i>n</i> = 127)			
COM vs. COL	-5.298	492	≤0.0001
EXT vs. COL	-7.507	492	≤0.0001
EXT vs. COM	-2.305	492	0.0216
NCOM vs. COL	-0.445	492	0.6567
NCOM vs. COM	4.903	492	≤0.0001
NCOM vs. EXT	7.138	492	≤0.0001
Southern species (<i>n</i> = 127)			
COM vs. COL	-4.615	469	≤0.0001
EXT vs. COL	0.163	469	0.8703
EXT vs. COM	4.573	469	≤0.0001
NCOM vs. COL	3.641	469	0.0003
NCOM vs. COM	8.361	469	≤0.0001
NCOM vs. EXT	3.311	469	0.0010

Notes: The categories include common (COM), common and extirpated (EXT), common and colonizing (COL), and present but not identified in any of the three common categories (NCOM). A total of 254 species documented at 856 CBC circles from 1975 to 2004 were considered in the analysis. (See *Methods* for details on the analysis and description of categories.)

north of Extirpation events. Hence, within species ranges, species were designated as Not Common at more CBC circles, and these circles tended to be located closer to the northern boundary of the range. In addition, colonization events were more prevalent at CBC circles and these tended to be located closer to the northern boundary of the range.

Based on the bootstrap-*t* method, in the northern portion of the study area, the proportion of CBC circles where species were designated as Common exceeded the proportion where species were designated as Not Common ($t = 2.592$, $P = 0.012$). In the southern portion of the study area the pattern was reversed, with the proportion of CBC circles where species were designated as Not Common being in the majority ($t = -7.915$, $P \leq 0.001$). In both the northern and southern portions of the study area, the proportion of CBC circles where species were designated as Colonized exceeded the proportion where the species were designated as Extirpated ($P \leq 0.001$).

The average latitude of CBC circles in the four categories based on the turnover analysis differed on average for species located in the northern portion of the study area (one-way ANOVA, $F_{3,492} = 27.339$, $P \leq 0.0001$), and differed on average for species located in the southern portion of the study area (one-way ANOVA, $F_{3,469} = 23.493$, $P \leq 0.0001$; Fig. 4B). Based on *t* tests of category pairs, several patterns were evident

(Table 2; Fig. 4B). For species located in the northern portion of the study area, CBC circles where species were identified as Not Common and CBC circles where species were identified as Colonized were located at similar latitudes on average. Both of these categories were north of circles where species were identified as Common followed by circles where species were identified as Extirpated. For species located in the southern portion of the study area, CBC circles where species were identified as Not Common were the farthest north. Circles where species were identified as Colonized and Extirpated were, on average, located at the same latitude, which was north of circles where species were identified as Common.

Latitudinal trends revisited

If we reapply the linear mixed model applied above, but with the six species experiencing extreme colonization and extirpation events removed, there was evidence for positive gains in maximum latitude ($t_{7190} = 3.302$, $P = 0.001$), positive gains in average latitude ($t_{7189} = 2.290$, $P = 0.0220$), and positive gains in the center of mass ($t_{7189} = 2.970$, $P = 0.0030$). Hence, after accounting for the effect of range size, the rate of increase in the northern boundary declined to ~ 1.36 km/yr (95% CI: 0.55 to 2.16 km/yr). After accounting for the effect of range size and the location of the northern boundary, the rate of increase in the center of occurrence declined to ~ 0.37 km/yr (95% CI: 0.05 to 0.69 km/yr) and the rate of increase in the center of abundance declined to ~ 0.89 km/yr (95% CI: 0.30 to 1.48 km/yr). Therefore, $\sim 8\%$ of the latitudinal trend for the northern boundary, 14% of the trend for the center of occurrence, and 18% of the trend for the center of abundance were explained by the presence of these six species.

Lastly, after removing the six species that experienced extreme events, differences in trends for the northern boundary and center of abundance documented for species with ranges located in the northern vs. southern portion of the study area remained unchanged. In addition, the spatial distribution of colonization and extirpation events and the relative location of species identified as Common and Not Common remained unchanged.

DISCUSSION

These findings provide broad-scale geographic and taxonomic evidence that poleward shifts in geographic ranges occurred for avian species wintering in North America from 1975 to 2004. Moreover, our findings suggest that the poleward movement of northern boundaries was paralleled by similar trends occurring within the interior of the range. Thus, the use of the northern boundary as an index of ecological change appears to be justified. However, the magnitude of the trends was not consistent across the three range components: trends for the northern boundary were larger on average and more variable relative to trends

documented for the center of the range. This outcome is to be expected, because range boundaries are inherently more dynamic relative to the center of the range (Brown et al. 1996, Gaston 2003). Nevertheless, this suggests that the use of the northern boundary as an index may be problematic for investigations using limited or biased samples.

We also found evidence that these trends differed based on the latitude of species' ranges, suggesting that shifts were not occurring uniformly across the study area. In addition, we found no evidence that migratory status promoted stronger associations with latitudinal trends. The lack of an association with migratory status suggests that dispersal abilities were not correlated with range shifts. This could reflect the highly vagile nature of birds independent of migratory behavior and the lack of strong territorial behavior for birds during the winter season. On the other hand, the majority of species examined in this study had overlapping winter and breeding ranges and, in addition, several species contained subspecies with different levels or forms of migratory behavior. In combination, these factors could have reduced the association between migratory status and latitudinal trends.

The natural history during the 20th century for the six species that experienced extreme turnover events suggests several possible explanations for these events. Populations for the five species that experienced extreme colonization events benefited from one or more of the following factors: introductions outside historic ranges, intensive population and habitat management by humans, regeneration of forests in the northeastern United States from abandoned agricultural lands, reductions in human persecution and pesticide use, and urban and suburban development (Elliott and Arbib 1953, Grier 1982, Eaton 1992, Hill 1993, Rosenfield and Bielefeldt 1993, Dugger et al. 1994, Buehler 2000, Steenhof et al. 2001–2002). Overall, there is evidence a variety of anthropogenic factors operating directly and indirectly on ecological and environmental systems in North America promoted these extreme colonization events (La Sorte and Boecklen 2005), with no evidence for climate change as a driver.

For the one species that presented an extreme extirpation event, a different scenario is evident. The Evening Grosbeak (*Coccothraustes vespertinus*) is an irruptive migrant into the eastern United States with high annual variation both in number and distribution, showing little fidelity to wintering sites in the United States (Gillihan and Byers 2001). Based on where these extirpation events occurred, our results suggest that this species was not migrating as regularly or as extensively into the northeastern United States from Canada during the second half of the survey period. This is supported by evidence that winter irruptions into the eastern United States have declined substantially since the mid 1980s (Gillihan and Byers 2001). This pattern could represent a stabilization of the winter range in Canada in

accordance with the overall northward shifts in ranges documented in this study, or could represent a stabilization caused by other nonclimatic biotic or abiotic factors.

Overall, these explanations point to the influence of regional anthropogenic drivers with evidence that climatic change was possibly involved with one species. With this species excluded, this conclusion is supported by the strength of these events and their localized occurrence, which would suggest the influence of intensive regional processes and not uniform global processes. This conclusion is also supported by evidence that, relative to trends on the northern boundary, a larger proportion of the trends for the center of the range, particularly for abundance, was explained by the presence of these species. The evidence suggests that these events were associated primarily with distributional changes occurring within ranges, and less with changes occurring on range boundaries, i.e., events that, due to the unique history of anthropogenic activities in the region, happened to be located in the northern portion of ranges, resulting in patterns that mimicked poleward shifts. Other investigations have found evidence that regional habitat structure acted in combination with climate change to promote or oppose certain aspects of distributional trends (Hill et al. 2001, Warren et al. 2001). Therefore, our findings support the conclusion that the outcome of the interaction of climate change and regional factors on distributional trends is defined by the biotic and abiotic features within a region, and how anthropogenic activities have directly or indirectly impacted these features.

When we reexamine our results after removing the six species that experienced extreme turnover events, evidence for positive latitudinal trends remained. The magnitudes of the trends were diminished but not substantially. However, other investigations have found evidence for similar trends with birds in Great Britain (Thomas and Lennon 1999, Hickling et al. 2006) and Finland (Brommer 2004) during approximately the same time period. Therefore, independent of extreme turnover events, our results agree with findings from other regions supporting the conclusion that these trends are global in nature.

Our findings also suggest that species are more common (i.e., occur more frequently annually) toward the center of the range vs. the northern boundary of the range. This conclusion is in agreement with other investigations where populations at range margins were less dense and more variable over space when contrasted with populations toward the center of the range (Hengeveld and Haack 1982, Brown 1984, Lawton 1993, Travis and Dytham 2004). What our findings add to our understanding of the structure and dynamics of geographic ranges is evidence that populations at range margins are also more variable over time. In other words, populations are more persistent over time toward the center of the range and less so toward the margins.

In conjunction with these findings was the spatial arrangement and relative proportion of extirpation and colonization events within species' ranges. Colonization and extirpation events tended to occur closer to the northern edge of the range, supporting the conclusion that range margins are more dynamic over time relative to the center of the range (Doherty et al. 2003). In addition, colonization events took precedence over extirpation events at the northern edge of the range, implying that colonization events drove the observed range shifts. In other words, colonization events "pushed" the northern margin of the range by promoting the presence of more stable or persistent populations over time on the northern boundary.

There was also evidence that these dynamics differed for species with ranges centered in the northern vs. southern portions of the study area (more exactly, the south-central region of the north temperate zone; Fig. 1). One factor that could explain these differences would be the variable influence of climate change within this region. However, there was also evidence the boundaries of the study area played a role. Specifically, species with ranges centered in the north were more likely to be represented by complete ranges, where species centered in the south were more likely to have ranges that were truncated by the southern boundary of the study area and/or the Gulf of Mexico. These differences likely promoted the association with changes in the center of abundance for northern species and changes in the northern boundary for southern species. However, our findings are somewhat counterintuitive; we would expect all aspects of the range to be less prone to northward movement in the south based on our predictions and the limitations of the study area. This suggests that changes in the northern boundary might indeed be more substantial for southern species. Overall, there is evidence that species wintering at different latitudes responded differently to the influence of climate change suggesting that species closer to the tropics experienced more substantial changes in northern boundaries and species closer to the center of the north temperate zone experienced more substantial changes in the center of abundance.

In summary, our findings suggest that geographic ranges shifted poleward due to the prevalence of colonization events on the northern boundary of ranges, driven by a combination of climate change and regional anthropogenic drivers. Therefore, processes operating at a variety of scales need to be considered when assessing ecological changes that are typically considered to represent the impact of climate change. This is particularly the case in regions where anthropogenic activities have directly or indirectly impacted species' habitats and populations. Where these regional anthropogenic drivers are lacking, trends will likely represent the effects of climate change more directly. Thus, using climate change as a blanket explanation in some regions could bias research or conservation efforts away from

considering the effect of regional factors, factors that could still be managed effectively to achieve conservation goals. In the end, however, regional anthropogenic drivers explained a relatively small proportion of observed poleward trends. We conclude that climate change, in association with regional drivers, will likely continue to shape contemporary biogeographical patterns, and the interaction between these two forces must be considered when documenting or modeling these patterns or when including these patterns in conservation assessments.

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APPENDIX

A table summarizing the associations and findings for all 254 avian species considered in the analysis (*Ecological Archives* E088-107-A1).