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Research Paper

Evaluating the efficacy of eBird data for modeling historical population trajectories of North American birds and for monitoring populations of boreal and Arctic breeding species

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ABSTRACT. Historic population trajectories for most North American bird species are largely unknown for years prior to circa 1970. Additionally, current estimates of population trajectories of boreal and Arctic breeding species are imprecise or biased because of lack of coverage by Breeding Bird Survey (BBS) routes in that region. Citizen science data, in particular eBird data, could fill these information gaps. Bayesian regression models of eBird data were used to estimate population trajectories of 22 boreal or Arctic breeding species of songbirds, 4 migratory songbird species that breed in eastern North America, and 2 species of raptors whose populations crashed due to the pesticide DDT. Models used range-wide data from the U.S. and Canada for spring migration/breeding, fall migration, and winter. To evaluate the model results, comparisons were made between eBird models from different seasons, between eBird indices and area defoliated by spruce budworm (*Choristoneura fumiferana*), and between eBird, BBS, and Christmas Bird Count (CBC) annual indices and trends. Population trajectories were positively correlated between seasons for most of the species analyzed based on correlations between annual indices, magnitude of trends, and residuals from trend models. Of the species analyzed, those most often associated with spruce budworm outbreaks had the strongest correlations between eBird annual indices and area defoliated by spruce budworm in the boreal forest. Annual indices from eBird models were positively correlated with BBS for most species, and trends calculated through the annual indices from eBird models were strongly correlated with those from the BBS for spring ($r = 0.73$, $n = 25$, $P < 0.0001$), fall ($r = 0.64$, $n = 25$, $P = 0.0005$), and winter ($r = 0.81$, $n = 9$, $P = 0.0084$), and winter eBird trends were correlated with those from the CBC ($r = 0.64$, $n = 12$, $P = 0.0252$). The results suggest eBird analyses could be an important complement to the BBS, CBC, and other surveys for assessing the status of bird species in North America, and that historic population trajectories could be estimated with additional historic eBird checklists.

Évaluation de l'efficacité des données eBird pour la modélisation des trajectoires historiques des populations d'oiseaux nord-américains et pour la surveillance des populations d'espèces nichant dans les régions boréales et arctiques

RÉSUMÉ. Les trajectoires historiques des populations de la plupart des espèces d'oiseaux nord-américains étaient en grande partie inconnues jusqu'aux environs de 1970. En outre, les estimations actuelles des trajectoires des populations d'espèces nichant dans les régions boréales et arctiques sont imprécises ou biaisées en raison d'un manque de couverture par les routes du Breeding Bird Survey (BBS) dans ces zones. Les données scientifiques recueillies par les citoyens, notamment les données eBird, pourraient combler ces lacunes d'informations. On a utilisé des modèles de régression bayésienne des données eBird pour estimer les trajectoires des populations de 22 espèces d'oiseaux chanteurs nichant dans les régions boréales ou arctiques, de 4 espèces d'oiseaux chanteurs nichant dans l'est de l'Amérique du Nord et de 2 espèces de rapaces dont les populations ont été décimées par l'utilisation du pesticide DDT. Les modèles utilisaient des données à l'échelle de l'habitat depuis les États-Unis et le Canada pour la migration/nidification de printemps, la migration d'automne et l'hiver. Afin d'évaluer les résultats des modèles, des comparaisons ont été réalisées entre des modèles eBird recueillis lors des différentes saisons, entre les indices eBird et une zone défoliée par la tordeuse des bourgeons de l'épinette (Choristoneura fumiferana), et entre les indices annuels et les tendances d'eBird, BBS et Christmas Bird Count (CBC). Les trajectoires des populations ont été corrélées de manière positive entre les saisons pour la plupart des espèces analysées en fonction des corrélations entre les indices annuels, la magnitude des tendances et les effets résiduels des modèles de tendance. Sur les différentes espèces analysées, celles qui étaient le plus souvent associées aux épidémies de tordeuse des bourgeons de l'épinette présentaient les plus fortes corrélations entre les indices annuels eBird et ceux de la zone défoliée par la tordeuse des bourgeons de l'épinette dans la forêt boréale. Les indices annuels obtenus grâce aux modèles eBird ont été corrélés de manière positive avec ceux du BBS pour la plupart des espèces, et les tendances calculées par le biais des indices annuels provenant des modèles eBird ont été fortement corrélés avec ceux du BBS pour le printemps ($r = 0{,}73$, $n = 25$, $P < 0{,}0001$), l'automne ($r = 0{,}64$, $n = 25$, $P = 0{,}0005$) et l'hiver ($r = 0{,}81$, $n = 9$, $P = 0{,}0084$), et les tendances eBord d'hiver ont été corrélées avec celles du CBC ($r = 0{,}64$, $n = 12$, $P = 0{,}0252$). Les résultats suggèrent que les analyses eBird pourraient constituer un complément important de celles du BBS, du CBC et d'autres organismes d'étude pour évaluer la situation des espèces ornithologiques en Amérique du Nord, et que les trajectoires historiques des populations pourraient être estimées à l'aide de listes de contrôle historiques supplémentaires d'eBird.

Key Words: *boreal forest; breeding bird survey; Christmas bird count; citizen science; eBird; population trend*

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INTRODUCTION

Conservation and management decisions should be made using the best available knowledge regarding the population status of the species of concern. Since the mid-1960s, population sizes of many bird species in the U.S. and Canada have been reliably tracked using data from the North American Breeding Bird Survey (hereafter BBS; Sauer et al. 2013). Species not effectively monitored using that protocol include nocturnal, rare, cryptic, secretive, shorebird, water-bird, marsh-bird, and boreal and Arctic breeders (e.g., Betts et al. 2007, Harris and Haskell 2007, NABCI 2012, ECCC 2014*a*). For these species, other sources of data are used to model population trends, such as the Christmas Bird Count (hereafter CBC), bird observatories in the U.S. and in the Canadian Migration Monitoring Network, or various taxon-specific surveys, e.g., Waterfowl Breeding and Population Habitat Survey (hereafter WBPHS), the Mid-Winter Waterfowl Survey (hereafter MWWS), the International Shorebird Survey (hereafter ISS) and related surveys, the Nocturnal Owl Survey, the Nightjar Survey Network, the Marsh Monitoring Program, and Colonial Waterbird Counts. Broad scale syntheses of national and international bird population trends such as the Partners in Flight Landbird Conservation Plan, the State of North America's Birds, and the Status of Birds in Canada rely upon data from the aforementioned surveys, and influence conservation and management decisions and funding strategies (ECCC 2014*a*, NABCI 2016, Rosenberg et al. 2016). Despite all of these diverse efforts, two major deficiencies remain: population trend data only date back to the 1970s for most species, and boreal and Arctic breeding species are poorly monitored. Citizen science data, in particular the eBird project (http://www.ebird.org), could potentially help remedy these deficiencies.

Estimating historical population change is challenging given that most long-term monitoring programs were initiated in the late 1960s or more recently. The BBS is widely considered the most reliable source of population data in the U.S. and Canada, but it was only initiated in 1966 (Sauer et al. 2013). The CBC, the longest-running bird survey in the world, was launched in 1900, but is limited to species that winter in North America (Butcher 1990*a*). However, the early years of the CBC may not provide sufficient data to model population trends with confidence (Bock and Smith 1971, Schreiber and Schreiber 1973, Niven et al. 2004). Numbers of CBC count circles remained relatively low until the 1950s, which is also when methodologies were standardized between circles (Butcher 1990*a*, Butcher et al. 2005). Consequently, most contemporary studies that use CBC data to compute population trends focus on years subsequent to 1950 (e.g., Butcher 1990*b*, Sauer et al. 1996, 2004, Niven et al. 2004, Butcher et al. 2005, Soykan et al. 2016). The oldest bird observatory in North America, Long Point Bird Observatory, was established in 1961, and several other major bird observatories were founded that decade (Point Reyes, Whitefish Point, and Manomet). Of the taxa specific surveys, the longest running are the Mid-winter Waterfowl Survey and WBPHS (both 1955; USFWS 2016, 2017), the American Woodcock Singing Ground Survey (1968), and the ISS (1974). Most of the other taxa specific surveys were initiated in more recent times and do not provide long-term indices of populations. In short, there is very little population trend data for bird species prior to the 1950s, and for species that winter outside of North America, data can only be analyzed reliably back to circa 1970.

We argue that to fully assess population trends of any bird species, it would be beneficial to be able to model trajectories prior to 1970. Without a historical context for bird populations and an understanding of long-term population cycles, setting target populations for species may be somewhat arbitrary. For instance, for species with large-amplitude population cycles, such as spruce budworm (*Choristoneura fumiferana*) specialists, a longer time series is necessary to determine their status because the BBS only dates back to the last spruce budworm outbreak in the 1970s (Patten and Burger 1998). Similarly, populations of species that were adversely affected by DDT bottomed out in the 1970s, so there is no point of reference for historical population size.

Monitoring populations of bird species that nest in the Arctic and boreal forest also remains a challenge because their breeding areas are vast and remote with limited road access. Monitoring these species on the breeding grounds is logistically and financially challenging. For boreal and Arctic species that winter largely in the U.S. and Canada, the CBC provides insight into their population status (Dunn and Sauer 1997, Niven et al. 2004, Soykan et al. 2016). For boreal and Arctic species that winter further south, trend information is more limited. Data from bird observatories that capture and record observations of these species during spring and fall migrations provide the best published trend information; however, it is still an unresolved problem whether the data from these few sites are representative of populations range-wide (Francis and Hussell 1998, Lloyd-Evans and Atwood 2004, Dunn et al. 2006, Crewe et al. 2008, 2016).

It has been shown elsewhere that data from the citizen science project eBird can be used to model population trends and that these trends broadly agree with BBS in areas and time periods with many eBird checklists (Walker and Taylor 2017, Horns et al. 2018*a*). The eBird project collects checklists made by birdwatchers using a suite of both generalized and specialized protocol types that describe almost any potential birdwatching scenario (Sullivan et al. 2014). The checklists are permanently archived, and the data are accessible through the eBird website in summarized and raw formats. Though launched in 2002, the flexible protocol types used by eBird allow for historical checklists to be entered, provided that at a minimum a date and location are specified. Globally there are currently (July 2020) > 45.8 million checklists in the eBird database, with ~36.9 million of these from the U.S. and Canada. Rates of checklist submission continue to grow exponentially.

Walker and Taylor (2017) estimated long-term (1970-2015) population trajectories from eBird data that produced trends comparable to those from BBS data for 22 species that reach the northern edge of their range in southern Ontario, Canada, a region with high numbers of eBird checklists. That result prompted the question of whether a similar methodology (Walker and Taylor 2017) could be applied at a broader scale and over a longer time series. Horns et al. 2018*a* used checklists from a broader scale, the contiguous U.S., to model trends for 574 species, but focused on a shorter timespan (1997-2016) when numbers of checklists were high. Horns et al. 2018*a* found trend estimates broadly agreed between eBird and BBS, but there was a large variation between species in how well the trends agreed, and many species showed trends with opposite signs (Fogarty et al. 2018, Horns et al. 2018*a*, *b*). Although both Horns et al. 2018*a* and Walker and Taylor 2017 found that underlying patterns of abundance were captured for many species, refinement of these techniques is necessary to produce reliable population trends using eBird data. Although numbers of historical checklists in eBird are low and geographically biased, we anticipated that range-wide aggregation of checklists might produce sample sizes sufficient to determine if there is meaningful information in the historical data. Furthermore, aggregation of lists across the continent during spring and fall migration could provide representative samples despite pronounced geographic sampling bias, because most migratory species pass through at least some areas with high eBird coverage. Additionally, during the migratory period, birds far away from their breeding ranges pass through narrower migratory pathways, facilitating the estimation of continent-wide population indices.

The objectives of this study were twofold: (1) to explore the current eBird dataset to determine how far into the past population trajectories can be estimated and (2) to produce range-wide population trajectories of boreal and Arctic breeding species for which few other sources of data exist. Because both of these objectives aim to fill information gaps in existing monitoring strategies, direct comparisons to other data sources (to assess the validity of the method) are limited or nonexistent. We therefore reasoned that we could assess such validity via indirect methods. First, we predicted that if the methods were effective at dealing with biases inherent in the eBird data set, we would (across a suite of different species) see comparable population trajectories derived from data from different seasons (spring, fall, and winter). Second, we anticipated that patterns in population change of species with well-publicized patterns of population decline and rebound associated with the use and banning of DDT, e.g., Peregrine Falcon (*Falco peregrinus*), Bald Eagle (*Haliaeetus leucocephalus*), would broadly show the known patterns. Third, we predicted that species known to be associated with spruce budworm outbreaks, i.e., Cape May Warbler (*Setophaga tigrina*), Bay-breasted Warbler (*Setophaga castanea*), Tennessee Warbler (*Leiothlypis peregrina*), and Evening Grosbeak (*Coccothraustes vespertinus*), would show patterns of increase and decrease broadly in concordance with the known timing of those outbreaks in boreal Canada (Patten and Burger 1998). To further evaluate the methodology, we also undertook comparisons with published trends from BBS and CBC data for the years and species for which trends were available. Although not unequivocal, if the results from the models produced the expected patterns, we argue that longer-term analysis of population change may be possible, particularly with the inclusion of additional historic checklists into the eBird database. Such an effort would provide additional and valuable insight into population trends for boreal (and other) species over a longer time frame than was heretofore possible.

METHODS

Species, areas, and dates included

Twenty-two species of songbirds that breed in the boreal forest or the Arctic, four songbird species that breed south of the boreal forest, and two raptor species were selected for analysis based on several criteria (Table 1). The three warbler species most associated with spruce budworm outbreaks (Cape May Warbler, Tennessee Warbler, and Bay-breasted Warbler) and Evening Grosbeak were selected initially with the expectation that populations of these four species would show similar long-term cycles, and should be positively correlated with spruce budworm outbreaks (Patten and Burger 1998, Venier et al. 2009). The additional 18 boreal or Arctic species were selected using the Status of Birds in Canada website (ECCC 2014*a*) and the Partners in Flight Landbird Conservation Plan 2016 Revision (Rosenberg et al. 2016). Nine of these species were selected because trend reliability scores were either low or deficient in the Status of Birds in Canada 2014. These reliability scores were based on analysis of data from various surveys that were appropriate for the species (BBS, CBC, etc.), and were scored on the precision of estimated trends, the proportion of seasonal geographic range covered by the surveys, and the reliability of the survey for the species in question (ECCC 2014*a*). Eight additional boreal and Arctic species were selected because they were labeled as “watch list” or “common species in steep decline” by the Partners in Flight Landbird Conservation Plan 2016 Revision (Rosenberg et al. 2016). Because the eight species selected were presumed to be declining a priori, we also selected three species of northern-breeding songbirds for which BBS data indicated survey-wide increases to ensure that results showing declines were not due to systematic bias: Magnolia Warbler (*Setophaga magnolia*; boreal forest), Northern Parula (*Setophaga americana*; eastern forest), and Black-throated Blue Warbler (*Setophaga caerulescens*; eastern forest; Sauer et al. 2017). Two additional eastern forest species with reliable trends in BBS were selected, of which Blue-winged Warbler (*Vermivora cyanoptera*) was stable and Golden-winged Warbler (*Vermivora chrysoptera*) was decreasing.

Finally, two raptor species were selected for which long-term population trajectories are widely known, Bald Eagle and Peregrine Falcon. Populations of both species were critically low in North America in the 1960s and 1970s due to DDT contamination, but rebounded after DDT was banned and recovery plans were implemented (USFWS 2003, 2009).

The eBird basic datasets from the August 2016 data release were downloaded for the United States (excluding Hawaii) and Canada, and filtered to include all complete checklists reporting greater than one species (Cornell Lab of Ornithology 2016). The checklists were divided into seasons and analyzed separately for each species. Spring migration and breeding (hereafter Spring) included checklists from March through June (inclusive), fall migration included lists from August through November (inclusive), and for species that winter in the United States and Canada lists from December through February (inclusive) were used. Checklists from 1928 through 2015 were included in the models. Data from 2016 were incomplete because the fall and winter seasons had not yet occurred, and checklists prior to 1928 were considered too sparse to be included.

For each species and season, unique geographic areas and date ranges were used to eliminate checklists from areas and dates from which that species rarely or never occurred. For each state/province, the total number of checklists submitted and the number of checklists reporting each species were calculated by season. If, across the entire time series, there were 10 or fewer

Table 1. Species analyzed, including their Partners in Flight (PIF) status in Rosenberg et al. 2016, trend reliability from Environment and Climate Change Canada 2014, Canadian responsibility based on the percent of their breeding range that falls within Canada, and breeding areas. Partners in Flight's status abbreviations are watch list (WL) and common species in steep decline (CSSD).

Species	PIF Status	Trend Reliability	Canadian Responsibility	Breeding Area
Bald Eagle (*Haliaeetus leucocephalus*)		High	Moderate	Widespread
Peregrine Falcon (*Falco peregrinus*)		High	Moderate	Widespread
Olive-sided Flycatcher (*Contupus cooperi*)	WL	High	High	Boreal Forest
Yellow-bellied Flycatcher (*Empidonax flaviventris*)		Low	Very High	Boreal Forest
Least Flycatcher (*Empidonax minimus*)	CSSD	Medium	Very High	Eastern and Boreal Forests
Gray-cheeked Thrush (*Catharus minimus*)		Low	Moderate	Boreal Forest
Lapland Longspur (*Calcarius lapponicus*)		Low	Moderate	Arctic
Smith's Longspur (*Calcarius pictus*)		Deficient	High	Arctic
Golden-winged Warbler (*Vermivora chrysoptera*)	WL	Medium	Low	Eastern Forest
Blue-winged Warbler (*Vermivora cyanoptera*)		High	Low	Eastern Forest
Tennessee Warbler (*Oreothlypis peregrina*)		Low	Very High	Boreal Forest
Connecticut Warbler (*Oporornis agilis*)	WL	Medium	Very High	Boreal Forest
Cape May Warbler (*Setophaga tigrina*)	WL	Medium	Very High	Boreal Forest
Northern Parula (*Setophaga americana*)		High	Moderate	Eastern Forest
Magnolia Warbler (*Setophaga magnolia*)		Medium	Very High	Boreal Forest
Bay-breasted Warbler (*Setophaga castanea*)		Medium	Very High	Boreal Forest
Blackpoll Warbler (*Setophaga striata*)	CSSD	Deficient	High	Boreal Forest
Black-throated Blue Warbler (*Setophaga caerulescens*)		High	High	Eastern Forest
Canada Warbler (*Cardellina canadensis*)	WL	Medium	Very High	Boreal Forest
Wilson's Warbler (*Cardellina pusilla*)	CSSD	Medium	Moderate	Boreal Forest
Le Conte's Sparrow (*Ammodramus leconteii*)	WL	Low	Very High	Grasslands and Boreal Wetlands
American Tree Sparrow (*Spizelloides arborea*)	CSSD	Medium	High	Arctic
White-crowned Sparrow (*Zonotrichia leucophrys*)		Low	High	Arctic
Harris's Sparrow (*Zonotrichia querula*)	WL	High	Very High	Boreal Forest
Rusty Blackbird (*Euphagus carolinus*)	CSSD	High	Very High	Boreal Forest
Common Redpoll (*Acanthis flammea)*		Low	Low	Arctic
Pine Siskin (*Spinus pinus*)	CSSD	Low	High	Boreal Forest
Evening Grosbeak (*Coccothraustes vespertinus*)	WL	High	High	Boreal Forest

checklists reporting a species or the frequency of checklists reporting that species was less than 0.001 in a given state/province, then checklists from that entire state or province were excluded from the analysis for that species and season. For the remaining states and provinces, 1% and 99% date quantiles were calculated for occurrence of each species by season, and all checklists from that state/province outside of the date quantiles were discarded if the date quantiles were more than 10 days from the beginning or end of the season (to avoid discarding data for species that were already or still present in the study area at the beginning or end of the season). Finally, checklists from each state/province were grouped into 40 × 40 km grid cells and cells in which a species had never been reported during a season across all years were excluded from the analysis for that species and season.

Data filtering and statistical models

The resulting data were then further filtered in a similar manner as Walker and Taylor (2017). To facilitate the inclusion of older historical and incidental checklists, all complete checklists of greater than one species were included regardless of effort information included. Shared checklists were reduced to a single checklist and assigned to the first observer associated with the list. Specialized checklist protocol types were reclassified to correspond to one of the three primary protocol types (traveling count, stationary count, or incidental) based on the effort information included, but several protocol types were excluded that did not fit within the framework of the study (see Appendix 1 for more details). Although current eBird submissions force all incidental lists to be flagged as incomplete, the original checklist submission process allowed for complete incidental lists, so these were included in the analysis.

Bayesian multilevel regression models were fit to the data for each species separately in both spring and fall, and in winter for those species which winter in the U.S. and Canada using package brms (version 1.6.1) in R Statistical programming language (version 3.2.5; R Core Team 2016, Bürkner 2017). The function brm in package brms uses syntax similar to that of package lme4 (Bates et al. 2015) in R, but uses the program Stan on the back end to specify the model (Stan Development Team 2017). Stan uses the Hamiltonian Markov chain Monte Carlo method and No-U-Turn Sampler to implement the models (Hoffman and Gelman 2014). We employed this method because models using lme4 converged inconsistently, which appeared to be an issue with using lme4 for exceptionally large datasets. Parameter estimates from models using brms were very similar to those from lme4, but the models converged for all but three of the species/season combinations.

Probability of occurrence on a checklist with a Bernoulli error distribution was used as the response variable in each model to facilitate incorporation of many checklists pre-2000 that lacked count data. The use of occurrence on a checklist as a response instead of abundance data may produce biased results for some species, especially for common and flocking species because the change in occurrence on checklists may not capture changes in abundance for those species. However, given the differences in sample size between checklists with occurrence data and checklists with count data, we opted to use occurrence for the response.

Year was fit as a factor to generate independent indices for each year, allowing for expected cyclical and other nonlinear patterns of occurrence across the time series. Years prior to 1970 were combined into bins of three years to boost sample sizes and decrease computation times. Any year or year bin with fewer than 20 checklists or zero observations of the target species was removed to facilitate model fitting. Although removing years with zero observations of the target species may introduce some negative bias in trend estimates, we believe that data from these years are simply deficient for producing annual indices. Very few years, if any, were removed for most species, and years removed were mostly from the 1920s and 1930s. The reference year for the year factor was set to 2015 because that was the year with the most data for each species. An interaction between latitude and a quadratic term for date accounted for differences in timing of peak migration based on latitude within a season because the data spanned such large geographic areas. The number of species included on a checklist was used as a surrogate for effort (as in Roberts et al. 2007, Szabo et al. 2010, Walker and Taylor 2017, and Horns et al. 2018*a*), and the interaction with protocol type allowed for differing rates of species accumulation by protocol type.

An observer score was calculated using similar methods as used by Kelling et al. (2015), by using a random slope term in a global mixed effects model to estimate a separate species accumulation rate for each observer. Generalized linear mixed effects models using Poisson error terms were fit within each season using package lme4 (version 1.1-11) in the R (version 3.2.5) Statistical programming language (Bates et al. 2015, R Core Team 2016). The number of species on a checklist was the response variable. Only checklists including effort were used to generate the observer scores. Species accumulation was modeled by including log (checklist duration + square root of checklist duration) as a fixed effect. A quartic polynomial for time of day was also included to account for assumed peaks in species detectability at dawn and dusk. A random intercept term was included using each unique combination of state/province and month to account for differing number of species available for detection by region and month. Finally, a random slope term was included allowing for a differing rate of species accumulation for each observer. The random slope effects (observer scores) were extracted for each observer and were included as continuous fixed effect in the occurrence models. Observers that had never entered a checklist with effort were assigned an observer score of 0, which was equivalent to the overall mean rate of species accumulation. Assigning mean observer scores for observers who had never entered checklists with effort could introduce bias because historical lists were more likely to lack effort information. Thirteen percent of observers in the pre-1970 years lacked effort information compared to five percent post-1970. However, we did not want to expunge these historical checklists from these observers because sample sizes were already low. Much of the effect of observer was likely accounted for by including the number of species on a checklist as a fixed effect already, so we were not overly concerned with setting these missing data points to the mean for all observers. To verify that the observer score models worked as intended, we compared distributions of observer scores for all eBird regional editors in the U.S. and Canada to scores from the other observers. eBird regional editors are expert bird-watchers who vet eBird data submissions in their geographic area of expertise. We found that the mean score of eBird regional editors was higher and the distribution much narrower than those of all other eBird observers, suggesting that the method was generally effective.

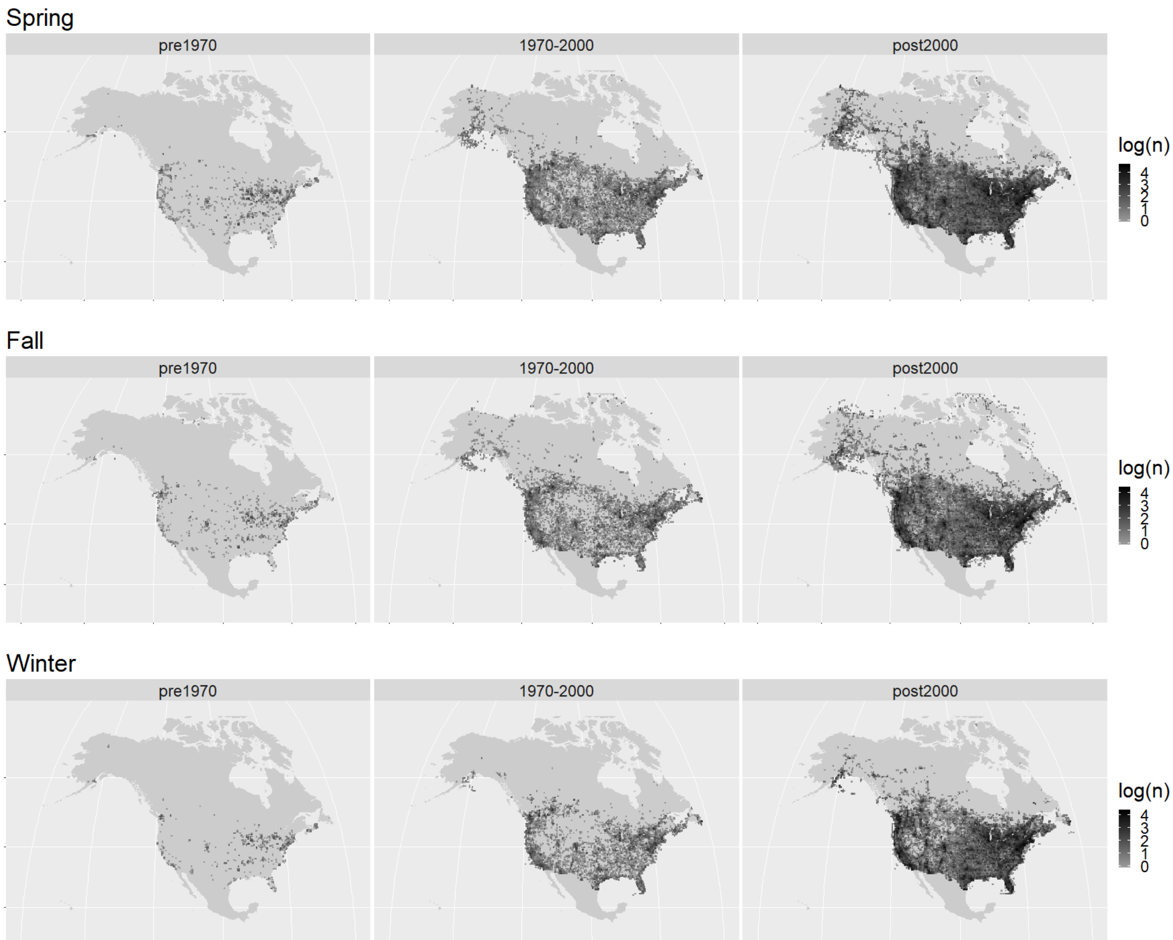
A random effect for geographic area (40 × 40 km cell) was included in the occurrence models to account for differences in frequency of occurrence by region and to account for geographic heterogeneity in checklist submission rates over time (Roy et al. 2012, Isaac et al. 2014). Although smaller grid cells or specific locations might be preferable to account for more habitat specific differences in occurrence, the numbers of random effects to be estimated at that scale exceeded the capacity of our computing infrastructure. Including a random effect of geographic area allows for checklists from anywhere in the species' range to be incorporated into the models. The random intercept term can be thought of as a measure of how frequently the species of interest was recorded in each grid cell and is strongly influenced by recent years with prolific data. Although this method does not allow for estimating regional or grid cell differences in population trajectories, it facilitates the incorporation of scattered checklists from historic times. Annual indices are most reflective of areas with the highest densities of checklists, but are still influenced by checklists from areas with lower densities. An alternative methodology would be to limit the study to areas with the highest numbers of historical lists, but this would eliminate much information from areas with high numbers of contemporary lists and few historic lists. Figure 1 depicts the geographic densities of checklists in eBird over three time periods (pre-1970, 1970-2000, post-2000) and in each season as of August 2016, and Appendix 2 displays the geographic density of checklists used for each individual model based on our filtering criteria over the same time periods. Appendix 3 provides model outputs regarding the geographic random effect term for each model, including effect size, error, rhat values and the number of 40 x 40 km grid cells used.

In summary, fixed effects terms in the models included: year (fit as a factor), an interaction between latitude and a quadratic polynomial fit to date, an interaction between the log of the number of species on a checklist and protocol type, and an observer skill score. A random effect was included for location using 40 × 40 km grid cell as the grouping variable. Equation 1 provides a summary of the model in the syntax used by the brm function used in R.

$$\begin{aligned}\text{occurrence}(0,1) = {} & \text{factor(year)} + \\ & \ln\text{(number of species on a checklist)} * \text{protocol type} + \\ & \text{latitude} * \text{poly(date, 2)} + \text{observer score} + \\ & (1|\ \text{40km grid})\end{aligned}$$

The defaults of improper flat priors were used for population level effects and student *t* priors with three degrees of freedom used for the group level effects. The default number of iterations (1000 warm-up, 1000 sample) were used in the models. The number of

Fig. 1. Geographic coverage of eBird checklists (n) used in the study by 40 x 40 km grid cell in log10 scale by season and time period (pre-1970, 1970-2000, and post-2000). Each species used a different subset of these checklists based on their geographic range and observed dates of occurrence (Appendix 2).



chains was set at two, which ran simultaneously on two processing cores.

Models for White-crowned Sparrow (*Zonotrichia leucophrys*) in winter, Bald Eagle in fall, and American Tree Sparrow (*Spizelloides arborea*) in spring did not converge with rhat values above 1.10, but the other 65 models converged. Rhat values were 1.13 for the intercept of White-crowned Sparrow in Winter, and 1.11 for the intercept of Bald Eagle in Fall and 1.11 for the grid cell random effects for American Tree Sparrow and White-crowned Sparrow. These were some of the models with the largest sample sizes (see Appendix 4 for sample sizes for each model). Annual indices generated from these three models are included in the results, based on the close agreement between trajectories from these models and those from other seasons for the same species, but should be interpreted with caution (see Appendix 5 for plots of annual indices from each model). Smith's Longspur (*Calcarius pictus*) data were much sparser than the other species included and many historical years lacked sufficient data for modeling. The species was still included in the analyses using the years with sufficient data based on the filtering criteria above, because it is considered a data deficient species based on criteria in ECCC 2014*a*. Posterior predictive checks (ppc) were performed to assess the fit of the models by using the pp_check function in package brms, a random subset of 3000 checklists from each model as the data, and 1000 samples from the posterior distribution for each. No ppc plots examined indicated that model fits were unreasonable.

Assessment of population trajectories

Annual indices and their estimated errors were calculated for each species in each season using fitted values from the models on the response scale of probability of occurrence on a checklist. The average latitude and average number of species per checklist were used as the new data for the fitted values, and the date was set as the peak date of occurrence. Additionally, to obtain population-level estimates, observer score was set to 0, the protocol type was set to traveling count, and random effects of geographic location were not estimated.

Several comparisons were made to evaluate the annual indices generated by the models, including: correlations between seasonal eBird trends and trajectories, correlations between spruce budworm specialists and area defoliated by spruce budworm, and correlations between eBird and BBS annual indices and trends.

Seasonal eBird trends and trajectories

Pearson correlations were calculated between seasons using annual indices from the eBird models to ascertain whether the trajectories agreed for each species. To compare magnitudes of underlying trends, models were fit through the annual indices for each species and season for the entire time series using beta regressions with logit links using the R package betareg (Cribari-Neto and Zeileis 2010). Trends were compared between seasons across species using Pearson correlations. Trends from eBird annual indices were also calculated from 1970 to present for comparison with BBS and CBC, and those trends were also compared between seasons and across species using Pearson correlations. To further assess the amount of agreement in population trajectory, beta regressions were fit for each species using the indices for all seasons combined with a fixed effect for season, to determine if residuals from these models were correlated between seasons. This allowed us to compare whether cyclical or other nonlinear patterns in the indices were correlated between seasons using Pearson correlations.

Spruce budworm specialists

Data on extent of area defoliated by spruce budworm in the boreal forest dating back to 1939 were obtained from the National Forest Pest Strategy Information System (NRCAN 2014). The number of hectares of moderate, moderate to severe, and severe defoliation were summed and used as an index of spruce budworm defoliation, and areas of light and trace defoliation were excluded. Years prior to 1970 were binned into groups of three years to match the eBird indices, and the mean defoliation index across the years in each group was used. Spearman rank correlations were calculated between annual indices of spruce budworm defoliation and annual indices from eBird models for each species in each season because the indices were on different scales.

eBird vs BBS annual indices and trends

Comparisons were made between annual indices from eBird and BBS data for those species that were detected frequently enough on BBS routes to produce indices. Survey-wide annual indices were downloaded from the U.S. Geological Survey's BBS website (Sauer et al. 2017). Annual indices were downloaded from the Canadian Trends Website (ECCC 2014*b*) for three species that were not modeled by Sauer et al. (2017) because of poor coverage on BBS routes. Breeding Bird Survey indices from the years 1970-2015 were compared to annual indices from the eBird models using weighted Pearson correlations, with the inverse of the sum of the variance around each pair of BBS and eBird annual indices as the weights. Because BBS indices are shrunk toward a trend line as opposed to being estimated as individual factor levels as in the eBird models, they underestimate interannual variation in the data. As such, they, and the associated p-values, should be interpreted with caution. We provide them primarily to see whether the two types of indices broadly followed the same pattern.

Trends on a scale of annual percent change and associated confidence intervals were calculated for each species and season by fitting beta regressions with logit links using the R package betareg (Cribari-Neto and Zeileis 2010) to the annual indices from the eBird models between 1970 and 2015, for comparison with BBS and CBC data. This was done with the annual indices rather than raw eBird data because the imbalance in checklists between recent and historic times would yield trends that were almost entirely influenced by the most recent years. For comparison, trend estimates from survey-wide BBS data were downloaded from the BBS website (Sauer et al. 2017), and trends for three additional species not modeled by Sauer et al. (2017) were obtained from the Canadian Trends Website (ECCC 2014*b*). For species that winter in the U.S. and Canada, trends calculated from CBC data were also compared (Soykan et al. 2016). Pearson's correlation coefficient was calculated to test if the magnitude of trend estimates from eBird data were correlated to those from BBS and CBC data. We acknowledge that annual indices and trends were calculated using different underlying model structures and response types (count vs occurrence) for the BBS and CBC than we used for the eBird data; however, we were primarily interested in the general level of agreement between datasets rather than making a formal comparison. A formal comparison of trends derived from the three datasets should focus on geographic regions with high numbers of eBird checklists and good coverage of BBS routes and CBC circles.

RESULTS

Seasonal eBird trends and trajectories

Visual inspection of plots of annual indices for each species and season indicated that there is some level of agreement between population trajectories from different seasons in eBird for most species (Appendix 5). For each species, we fit LOESS smooths with spans of 0.2 through the annual indices for each season to aid interpretation of population trajectories over time. Correlation coefficients between spring and fall annual indices were positive for all but two of the species analyzed, and were positive for all species when spring and winter, and fall and winter were compared (Table 2). The mean correlation coefficient across species was 0.36 between spring and fall, 0.68 between spring and winter, and 0.48 between fall and winter. Trends calculated from the annual indices using the entire time series were highly correlated across species between spring and fall (r = 0.70, n = 28, P < 0.0001), spring and winter (r = 0.83, n = 12, P = 0.0007), and fall and winter (r = 0.89, n = 12, P = 0.0001; Fig. 2, Table 3). Trends calculated from annual indices from 1970 to 2015 for comparison with BBS and CBC were also strongly correlated across species between spring and fall (r = 0.87, n = 28, P < 0.0001), spring and winter (r = 0.95, n = 12, P < 0.0001), and fall and winter (r = 0.89, n = 12, P = 0.0001; Fig. 3, Table 4). Correlations of residuals from trend models fit through the seasonal data were largely in the positive direction, and some species with obvious nonlinear patterns over time showed strong correlations (Table 5). Overall, the correlations between residuals suggest that for many species, the eBird dataset is able to track population trajectories beyond what was explained by the underlying trends.

Table 2. Coefficients and *P* values for correlations between seasonal population trajectories between 1928 and 2015 from models using eBird data, in descending order by strength of correlation between spring and fall data. Correlations between spring and fall, spring and winter, and fall and winter eBird data are included in separate columns. See Table 1 for scientific species names.

	Spring vs Fall		Spring vs Winter		Fall vs Winter	
Species	*r*	*P*	*r*	*P*	*r*	*P*
Peregrine Falcon	0.85	< 0.0001	0.73	< 0.0001	0.74	< 0.0001
American Tree Sparrow	0.84	< 0.0001	0.90	< 0.0001	0.92	< 0.0001
Bald Eagle	0.70	< 0.0001	0.97	< 0.0001	0.95	< 0.0001
Bay-breasted Warbler	0.68	< 0.0001				
Rusty Blackbird	0.67	< 0.0001	0.36	0.0045	0.42	0.0009
Evening Grosbeak	0.63	< 0.0001	0.88	< 0.0001	0.65	< 0.0001
Cape May Warbler	0.61	< 0.0001				
Le Conte's Sparrow	0.58	< 0.0001	0.18	0.2070	0.27	0.0654
Canada Warbler	0.48	0.0001				
Blue-winged Warbler	0.48	0.0002				
Lapland Longspur	0.39	0.0025	0.49	0.0001	0.43	0.0008
Wilson's Warbler	0.38	0.0024				
White-crowned Sparrow	0.37	0.0041	0.77	< 0.0001	0.36	0.0064
Harris' Sparrow	0.36	0.0082	0.81	< 0.0001	0.61	< 0.0001
Tennessee Warbler	0.35	0.0055				
Least Flycatcher	0.32	0.0112				
Blackpoll Warbler	0.32	0.0126				
Black-throated Blue Warbler	0.29	0.0260				
Yellow-bellied Flycatcher	0.28	0.0304				
Olive-sided Flycatcher	0.24	0.0678				
Gray-cheeked Thrush	0.20	0.1181				
Northern Parula	0.16	0.2094				
Pine Siskin	0.13	0.3234	0.59	< 0.0001	0.06	0.6348
Connecticut Warbler	0.11	0.4378				
Golden-winged Warbler	0.09	0.5237				
Magnolia Warbler	0.04	0.7760				
Common Redpoll	-0.13	0.3717	0.77	< 0.0001	0.03	0.8172
Smith's Longspur	-0.23	0.4302	0.69	0.0002	0.28	0.3203

Spruce budworm specialists

The spruce budworm specialists in this study (Bay-breasted Warbler, Cape May Warbler, Tennessee Warbler, and Evening Grosbeak) all showed positive correlations with the number of hectares defoliated by spruce budworm, and, of the 28 species modeled, were the species with the strongest correlations (Table 6; Patten and Burger 1998, Venier et al. 2009). Smoothed population trajectories of these three warbler species and Evening Grosbeak showed some noticeable peaks in occurrence during outbreaks of spruce budworm (Fig. 4). For Magnolia Warbler, a species that has been shown in several studies to have a negative response to spruce budworm, there was no correlation between eBird annual indices and area defoliated by spruce budworm (Patten and Burger 1998, Venier et al. 2009; Table 6). Several other species showed moderate correlations between eBird data and spruce budworm that were not as strong as the spruce budworm specialists, but could indicate a relationship (Table 6). Several species, most notably the two species of raptors, White-crowned Sparrow, Northern Parula, and Least Flycatcher (*Empidonax minimus*; fall model), were negatively correlated with the spruce budworm index.

Fig. 2. Comparison plots of magnitude of population trends between spring eBird data and fall eBird data (A), spring eBird data and winter eBird data (B), and fall eBird data and winter eBird data (C). The x and y axes are mean annual percent change from 1928-2015, though the trends only date back as far as there were data available for each species and season. The error bars are 95% confidence intervals for the trend estimates. Colors represent the different groups of species analyzed (Arctic, Boreal, Eastern, and Raptor).

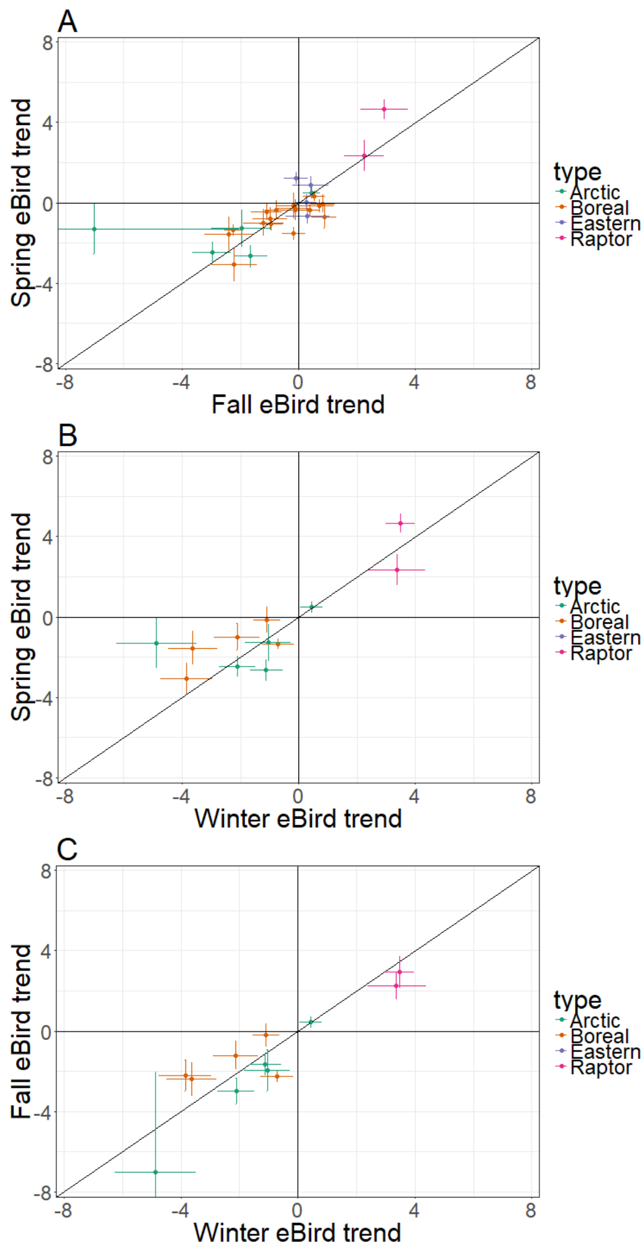


Table 3. Trends in annual percent change across the entire time series from 1928 to 2015 and associated confidence intervals for models of eBird data in spring, fall, and winter. See Table 1 for scientific species names.

	Spring		Fall		Winter	
Species	Trend	95% CI	Trend	95% CI	Trend	95% CI
American Tree Sparrow	-2.48	(-3.00, -1.97)	-2.97	(-3.63, -2.32)	-2.11	(-2.74, -1.48)
Bald Eagle	4.65	(4.18, 5.12)	2.94	(2.14, 3.74)	3.48	(2.98, 3.99)
Bay-breasted Warbler	-0.29	(-0.74, 0.15)	-0.13	(-0.70, 0.44)		
Blackpoll Warbler	-0.15	(-0.44, 0.14)	0.72	(0.22, 1.22)		
Black-throated Blue Warbler	0.02	(-0.39, 0.43)	0.26	(-0.11, 0.63)		
Blue-winged Warbler	0.87	(0.43, 1.31)	0.41	(-0.21, 1.03)		
Canada Warbler	-1.06	(-1.37, -0.75)	-0.94	(-1.33, -0.55)		
Cape May Warbler	-0.36	(-0.83, 0.12)	-0.11	(-0.71, 0.50)		
Connecticut Warbler	-0.79	(-1.33, -0.25)	-0.99	(-1.58, -0.40)		
Common Redpoll	-1.28	(-2.20, -0.36)	-1.95	(-2.99, -0.91)	-1.05	(-1.83, -0.27)
Evening Grosbeak	-3.08	(-3.88, -2.28)	-2.21	(-3.00, -1.42)	-3.85	(-4.74, -2.96)
Gray-cheeked Thrush	-1.54	(-1.85, -1.23)	-0.18	(-0.56, 0.21)		
Golden-winged Warbler	-0.66	(-1.07, -0.26)	0.30	(-0.44, 1.05)		
Harris's Sparrow	-1.55	(-2.40, -0.70)	-2.40	(-3.22, -1.58)	-3.64	(-4.48, -2.80)
Lapland Longspur	-2.66	(-3.21, -2.11)	-1.65	(-2.20, -1.10)	-1.12	(-1.67, -0.56)
Le Conte's Sparrow	-0.99	(-1.67, -0.31)	-1.21	(-1.91, -0.51)	-2.12	(-2.89, -1.35)
Least Flycatcher	-0.71	(-1.27, -0.14)	0.87	(0.43, 1.30)		
Magnolia Warbler	-0.37	(-0.65, -0.09)	0.37	(0.01, 0.73)		
Northern Parula	1.24	(0.94, 1.53)	-0.09	(-0.51, 0.32)		
Olive-sided Flycatcher	-0.35	(-0.8, 0.10)	-0.76	(-1.15, -0.36)		
Peregrine Falcon	2.33	(1.56, 3.10)	2.24	(1.56, 2.92)	3.36	(2.38, 4.35)
Pine Siskin	-0.13	(-0.78, 0.51)	-0.19	(-0.78, 0.39)	-1.09	(-1.55, -0.63)
Rusty Blackbird	-1.35	(-1.60, -1.09)	-2.24	(-2.54, -1.93)	-0.71	(-1.26, -0.16)
Smith's Longspur	-1.29	(-2.57, -0.02)	-7.03	(-12.01, -2.04)	-4.88	(-6.26, -3.49)
Tennessee Warbler	-0.04	(-0.49, 0.41)	0.83	(0.42, 1.25)		
White-crowned Sparrow	0.49	(0.21, 0.76)	0.44	(0.15, 0.73)	0.44	(0.06, 0.83)
Wilson's Warbler	0.32	(0.06, 0.58)	0.52	(0.14, 0.91)		
Yellow-bellied Flycatcher	-0.44	(-0.86, -0.02)	-1.09	(-1.62, -0.57)		

Table 4. Trends in annual percent change between 1970 and 2015 and associated 95% confidence or credible intervals for models of eBird data in spring, fall, and winter, Breeding Bird Survey (BBS) data, and Christmas Bird Count (CBC) data. See Table 1 for scientific species names.

	Spring		Fall		Winter		BBS		CBC	
Species	Trend	CI	Trend	CI	Trend	CI	Trend	CI	Trend	CI
American Tree Sparrow	-2.06	(-2.78, -1.35)	-1.60	(-2.31, -0.89)	-1.57	(-2.07, -1.07)	-1.39	(-10.8, 9.15)	-0.5	(0.4, -1.6)
Bald Eagle	5.73	(5.44, 6.02)	5.98	(5.74, 6.22)	4.50	(4.13, 4.86)	5.18	(4.17, 6.18)	4.6	(5.7, 3.4)
Bay-breasted Warbler	-2.51	(-3.13, -1.88)	-2.50	(-3.38, -1.62)			-0.25	(-2.07, 1.31)		
Black-throated Blue Warbler	0.23	(-0.25, 0.70)	-0.22	(-0.83, 0.40)			1.95	(1.27, 2.70)	0.3	(1.8, -1.2)
Blackpoll Warbler	-0.66	(-1.14, -0.17)	0.52	(-0.16, 1.21)			-4.85	(-12.02, -1.19)		
Blue-winged Warbler	-0.68	(-1.19, -0.17)	0.13	(-0.88, 1.15)			-0.70	(-1.34, 0.07)		
Canada Warbler	-2.00	(-2.6, -1.41)	-2.40	(-2.93, -1.87)			-2.05	(-2.81,-1.33)		
Cape May Warbler	-2.82	(-3.49, -2.16)	-3.45	(-4.27, -2.63)			-2.51	(-5.19, -0.30)	-1.8	(0.6, -4.2)
Common Redpoll	-2.18	(-3.94, -0.42)	-0.49	(-1.96, 0.98)	-1.69	(-3.11, -0.27)	-9.01	(-14.90, -2.22)	3.1	(5.6, -2.4)
Connecticut Warbler	-0.84	(-1.69, 0.01)	-1.11	(-2.16, -0.05)			-1.93	(-3.28, -0.51)		
Evening Grosbeak	-4.55	(-5.55, -3.54)	-5.14	(-5.94, -4.33)	-7.34	(-8.48, -6.2)	-6.36	(-18.59, -4.72)	-2.0	(0.3, -4.7)
Golden-winged Warbler	-2.36	(-2.88, -1.84)	0.48	(-0.68, 1.64)			-2.28	(-3.08, -1.47)		
Gray-cheeked Thrush	-2.08	(-2.78, -1.37)	-0.83	(-1.48, -0.18)			-0.13	(-10.10, 9.56)		
Harris's Sparrow	-2.02	(-3.11, -0.93)	-2.22	(-3.22, -1.21)	-2.32	(-3.00, -1.63)			-1.5	(-0.7, -2.4)
Lapland Longspur	-1.27	(-2.07, -0.47)	-1.07	(-1.61, -0.54)	-1.50	(-2.27, -0.72)			4.6	(8.2, -0.9)
Le Conte's Sparrow	-0.94	(-2.05, 0.18)	-0.88	(-1.84, 0.07)	-3.06	(-4.09, -2.03)	-2.59	(-4.03, -1.19)	1.1	(2.4, -0.2)
Least Flycatcher	-0.82	(-1.19, -0.44)	1.44	(0.92, 1.97)			-1.71	(-2.10, -1.33)	5.9	(8.8, 3.1)
Magnolia Warbler	-0.49	(-1.01, 0.04)	-0.01	(-0.40, 0.38)			0.87	(0.19, 1.57)	-2.2	(0.6, -8.3)
Northern Parula	1.63	(1.22, 2.04)	1.40	(1.00, 1.80)			1.11	(0.79, 1.42)	1.0	(1.9, 0)
Olive-sided Flycatcher	-0.81	(-1.14, -0.47)	-1.58	(-2.02, -1.14)			-3.10	(-3.97, -2.53)		
Peregrine Falcon	4.71	(4.09, 5.32)	4.17	(3.57, 4.78)	5.45	(4.74, 6.16)	2.77	(-1.61, 5.47)	4.4	(5.4, 2.9)
Pine Siskin	-1.36	(-2.42, -0.29)	-1.02	(-1.97, -0.06)	-1.64	(-2.55, -0.73)	-3.67	(-4.98,-2.57)	0.7	(2.7, -3.2)
Rusty Blackbird	-2.28	(-2.70, -1.86)	-2.17	(-2.76, -1.58)	-2.63	(-3.37, -1.9)	-3.53	(-6.19, -1.34)	-3.1	(-1.1, -5.7)
Smith's Longspur	-3.23	(-5.04, -1.42)	-7.03	(-12.01, -2.04)	-3.19	(-5.11, -1.27)			3.1	(9.9, -6.4)
Tennessee Warbler	-2.28	(-2.86, -1.71)	-0.39	(-0.92, 0.15)			-1.03	(-2.87, 0.61)	0.4	(3.6, -2.5)
White-crowned Sparrow	0.39	(0.09, 0.70)	0.68	(0.41, 0.95)	0.41	(0.12, 0.69)	-0.40	(-1.57, 0.14)	1.1	(1.9, 0.4)
Wilson's Warbler	-0.40	(-0.71, -0.09)	-0.84	(-1.15, -0.53)			-1.80	(-2.81, -1.12)	1.9	(3.3, 0.1)
Yellow-bellied Flycatcher	0.33	(-0.35, 1.01)	0.57	(-0.16, 1.29)			2.26	(0.56, 3.52)		

Fig. 3. Comparison plots of magnitude of population trends between spring eBird data and fall eBird data (A), spring eBird data and winter eBird data (B), and fall eBird data and winter eBird data (C). The x and y axes are mean annual percent change from 1970-2015. The error bars are 95% confidence intervals for the trend estimates. Colors represent the different groups of species analyzed (Arctic, Boreal, Eastern, and Raptor).

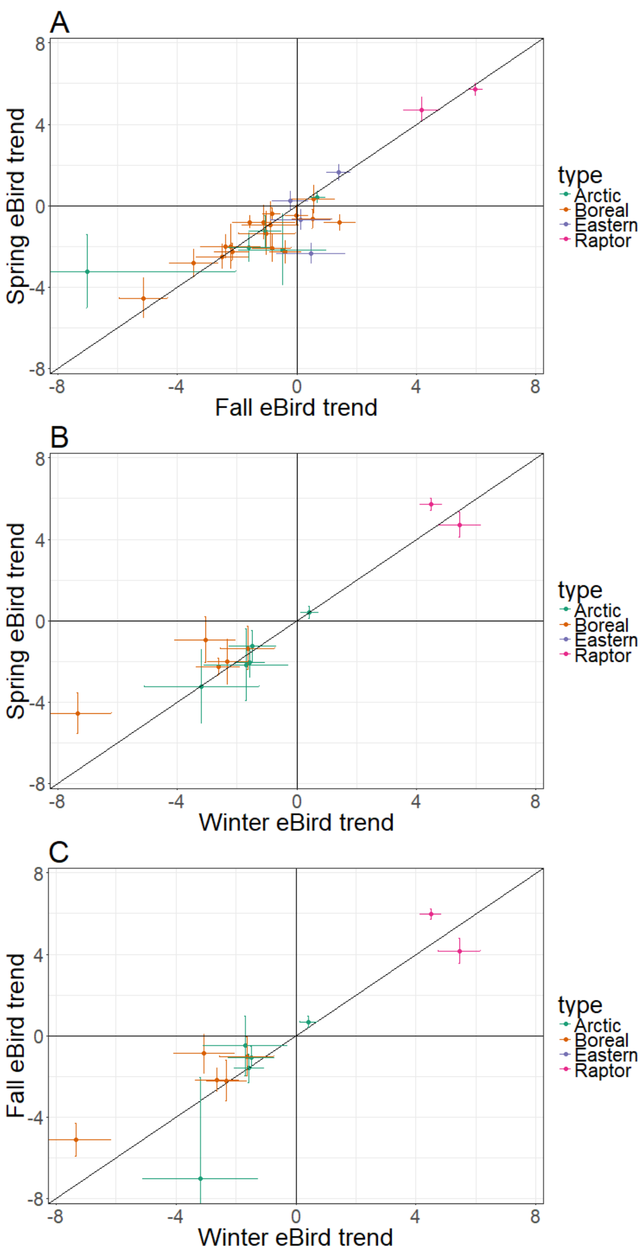
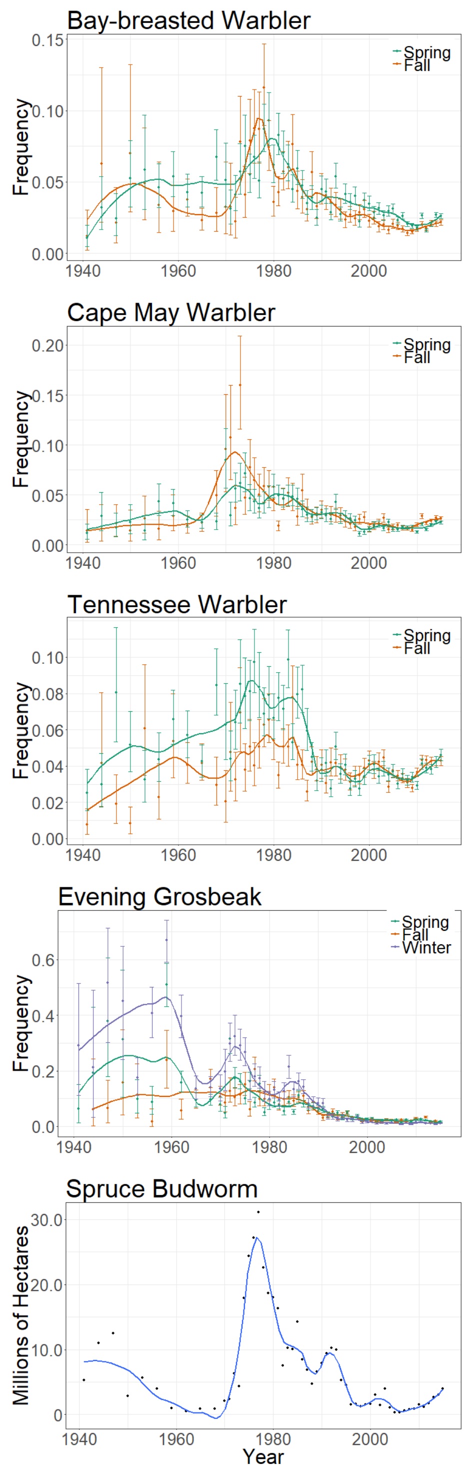


Fig. 4. Annual indices with smoothed trajectories (LOESS with a span of 0.2) from eBird models for the three species of warblers known to be associated with spruce budworm (*Choristoneura fumiferana*), Evening Grosbeak (*Coccothraustes vespertinus*), and the number of hectares defoliated by spruce budworm in the boreal forest. See Table 1 for scientific species names.



eBird vs BBS and CBC annual indices and trends

Correlations between annual indices from the eBird models and BBS data were mostly positive and there were few negative correlations (Table 7). The mean correlation coefficients across

Table 5. Coefficients and *P* values for correlations between residuals from trend models fit through the annual indices from eBird models for each species between 1928 and 2015, in descending order by strength of correlation between spring and fall data. Correlations between spring and fall, spring and winter, and fall and winter residuals from eBird trend models are included in separate columns. See Table 1 for scientific species names.

	Spring vs Fall		Spring vs Winter		Fall vs Winter	
Species	*r*	*P*	*r*	*P*	*r*	*P*
Peregrine Falcon	0.78	< 0.0001	0.69	< 0.0001	0.63	< 0.0001
Bay-breasted Warbler	0.68	< 0.0001				
Cape May Warbler	0.61	< 0.0001				
American Tree Sparrow	0.60	< 0.0001	0.82	< 0.0001	0.82	< 0.0001
Blue-winged Warbler	0.50	0.0001				
Bald Eagle	0.49	0.0001	0.48	0.0001	0.64	< 0.0001
Wilson's Warbler	0.38	0.0024				
Le Conte's Sparrow	0.37	0.0081	-0.01	0.9230	0.10	0.4811
Tennessee Warbler	0.36	0.0040				
White-crowned Sparrow	0.32	0.0114	0.78	< 0.0001	0.37	0.0048
Blackpoll Warbler	0.32	0.0132				
Black-throated Blue Warbler	0.30	0.0199				
Least Flycatcher	0.28	0.0314				
Evening Grosbeak	0.25	0.0620	0.72	< 0.0001	0.11	0.4208
Canada Warbler	0.20	0.1257				
Northern Parula	0.17	0.1881				
Yellow-bellied Flycatcher	0.12	0.3874				
Pine Siskin	0.12	0.3852	0.57	< 0.0001	-0.01	0.9292
Golden-winged Warbler	0.05	0.7233				
Olive-sided Flycatcher	0.05	0.7224				
Magnolia Warbler	0.04	0.7541				
Rusty Blackbird	0.01	0.9603	0.08	0.5523	0.08	0.5318
Harris's Sparrow	0.01	0.9659	0.68	< 0.0001	0.32	0.0232
Lapland Longspur	-0.12	0.3505	0.15	0.2558	0.08	0.5740
Gray-cheeked Thrush	-0.13	0.3196				
Connecticut Warbler	-0.13	0.3327				
Common Redpoll	-0.36	0.0097	0.74	<0.0001	-0.22	0.1244
Smith's Longspur	-0.42	0.1367	-0.39	0.0647	0.05	0.8530

species were 0.46 for spring indices, 0.32 for fall indices, and 0.55 for winter indices. eBird annual indices with smoothed trajectories plotted adjacent to those from BBS from 1970-2015 for each species are presented in Appendix 6.

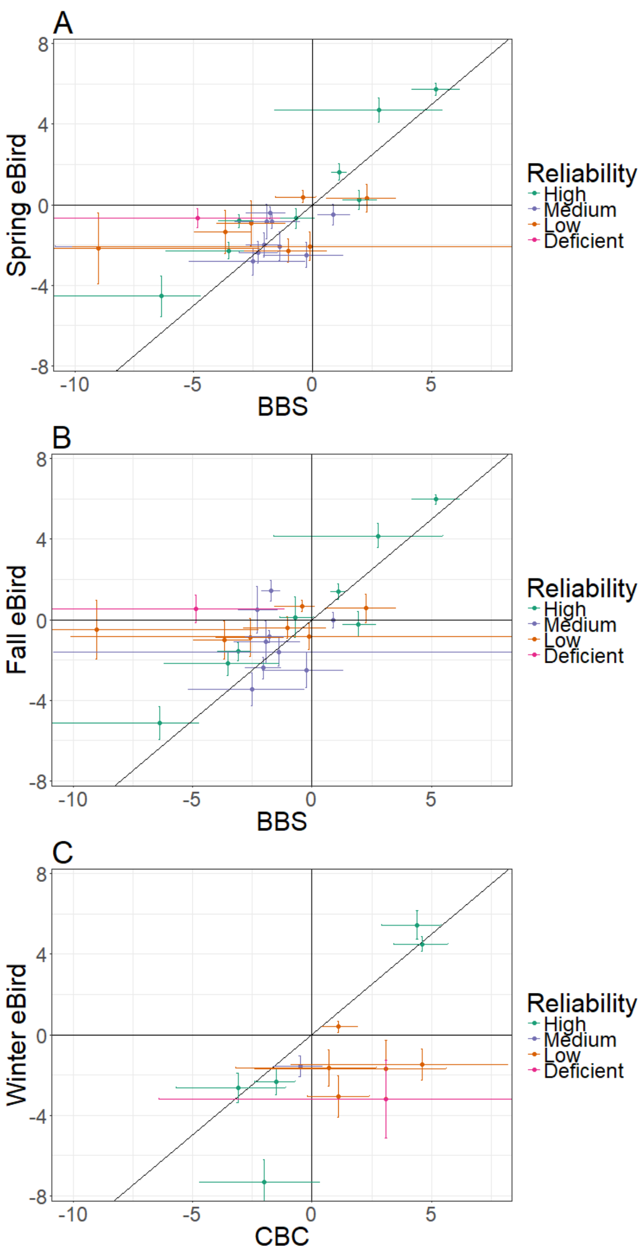
Trends calculated using the annual indices from the eBird models are presented alongside those from the BBS and CBC in Table 5. Pearson's correlation coefficients between eBird and BBS trend estimates were 0.73 (n = 25, $P < 0.0001$) for spring, 0.64 (n = 25, $P = 0.0005$) for fall, and 0.81 (n = 9, $P = 0.0084$) for winter (Figs. 5A and 5B). The Pearson's correlation coefficient between winter eBird trends and CBC trends was 0.64 (n = 12, $P = 0.0252$), but showed obvious bias between datasets with eBird data estimating more-negative trends (Fig. 5C). Residuals were not compared between datasets because the underlying trend models were different between eBird, BBS, and CBC.

For the boreal and Arctic breeding species, population trajectories mostly corroborated the trends from the BBS and CBC. For the four species with high trend reliability from either the BBS, i.e., Olive-sided Flycatcher (*Contopus cooperi*), or CBC, i.e., Evening Grosbeak, Harris's Sparrow (*Zonotrichia querula*), and Rusty Blackbird (*Euphagus carolinus*), there was agreement with eBird data, though the BBS indicated that Olive-sided Flycatchers were

Table 6. Coefficients and *P* values for correlations between annual indices from models using eBird data, and the number of hectares defoliated by spruce budworm (*Choristoneura fumiferana*) in the boreal forest, in descending order by strength of correlation. See Table 1 for scientific species names.

Species	Season	rho	*p*
Bay-breasted Warbler	Fall	0.711	< 0.0001
Cape May Warbler	Spring	0.628	< 0.0001
Cape May Warbler	Fall	0.533	< 0.0001
Bay-breasted Warbler	Spring	0.528	< 0.0001
Evening Grosbeak	Fall	0.507	0.0001
Tennessee Warbler	Spring	0.500	0.0001
Evening Grosbeak	Spring	0.486	0.0002
Le Conte's Sparrow	Fall	0.477	0.0005
Rusty Blackbird	Spring	0.469	0.0003
Evening Grosbeak	Winter	0.463	0.0004
Smith's Longspur	Winter	0.436	0.0084
Le Conte's Sparrow	Winter	0.401	0.0037
Canada Warbler	Fall	0.396	0.0027
Harris's Sparrow	Fall	0.396	0.0033
Olive-sided Flycatcher	Fall	0.390	0.0035
Wilson's Warbler	Fall	0.380	0.0041
Wilson's Warbler	Spring	0.352	0.0080
Lapland Longspur	Fall	0.338	0.0120
Golden-winged Warbler	Spring	0.333	0.0124
Tennessee Warbler	Fall	0.331	0.0130
Harris's Sparrow	Winter	0.329	0.0176
Rusty Blackbird	Winter	0.328	0.0148
Canada Warbler	Spring	0.319	0.0170
Smith's Longspur	Spring	0.300	0.1133
Connecticut Warbler	Fall	0.274	0.0476
Blue-winged Warbler	Spring	0.267	0.0470
Olive-sided Flycatcher	Spring	0.267	0.0474
Rusty Blackbird	Fall	0.264	0.0496
Pine Siskin	Winter	0.257	0.0565
American Tree Sparrow	Winter	0.240	0.0749
Pine Siskin	Fall	0.208	0.1236
Blue-winged Warbler	Fall	0.207	0.1358
Le Conte's Sparrow	Spring	0.200	0.1542
Harris's Sparrow	Spring	0.171	0.2119
American Tree Sparrow	Spring	0.171	0.2083
Gray-cheeked Thrush	Spring	0.168	0.2152
Pine Siskin	Spring	0.158	0.2454
American Tree Sparrow	Fall	0.137	0.3127
Least Flycatcher	Spring	0.126	0.3552
Gray-cheeked Thrush	Fall	0.106	0.4366
Lapland Longspur	Spring	0.090	0.5064
Common Redpoll	Fall	0.084	0.5560
Blackpoll Warbler	Spring	0.074	0.5878
Yellow-bellied Flycatcher	Spring	0.062	0.6498
Magnolia Warbler	Spring	0.049	0.7207
Common Redpoll	Spring	0.036	0.7976
Yellow-bellied Flycatcher	Fall	0.024	0.8628
Magnolia Warbler	Fall	0.023	0.8663
Connecticut Warbler	Spring	0.012	0.9329
Lapland Longspur	Winter	0.006	0.9678
Golden-winged Warbler	Fall	-0.011	0.9388
Common Redpoll	Winter	-0.063	0.6426
Black-throated Blue Warbler	Spring	-0.090	0.5077
Black-throated Blue Warbler	Fall	-0.171	0.2081
Blackpoll Warbler	Fall	-0.193	0.1545
Smith's Longspur	Fall	-0.196	0.4819
White-crowned Sparrow	Winter	-0.233	0.0897
Northern Parula	Fall	-0.288	0.0315
White-crowned Sparrow	Fall	-0.319	0.0170
White-crowned Sparrow	Spring	-0.419	0.0014
Peregrine Falcon	Fall	-0.431	0.0010
Bald Eagle	Winter	-0.434	0.0011
Peregrine Falcon	Winter	-0.437	0.0013
Bald Eagle	Fall	-0.448	0.0006
Northern Parula	Spring	-0.449	0.0006
Least Flycatcher	Fall	-0.449	0.0006
Bald Eagle	Spring	-0.454	0.0005
Peregrine Falcon	Spring	-0.501	0.0001

Fig. 5. Comparison plots of magnitude of population trends between spring eBird data and BBS data (A), fall eBird data and BBS data (B), and winter eBird data and CBC data (C). The x and y axes are mean annual percent change from 1970-2015. The error bars are 95% confidence intervals for the eBird trend estimates and credible intervals for the BBS and CBC trend estimates. Colors represent reliability of trends based on the Status of Birds in Canada 2014.



declining at a faster rate than was shown using eBird data. Trends for the eight boreal or Arctic breeding species with medium trend reliability also largely agreed between eBird and BBS, with overlapping trend estimates for Canada Warbler (*Cardellina canadensis*), Wilson's Warbler (*Cardellina pusilla*), Cape May Warbler, and Connecticut Warbler (*Oporornis agilis*). Trends for American Tree Sparrow, Bay-breasted Warbler, and Least Flycatcher did not agree between datasets, but Least Flycatchers showed declines that disagreed only in magnitude. For the 10 species with low or deficient trend reliability from BBS and CBC, it was difficult to assess agreement of trends because of wider credible intervals that often overlapped 0. None of these 10 species showed agreement between eBird and BBS based on a combination of sign and magnitude of trend.

The four warbler species that breed just south of the boreal forest showed some agreement between eBird and BBS trends. For the species with increasing trends in BBS, Northern Parula showed similar positive trends in eBird data, and Black-throated Blue Warblers eBird showed stable trends whose credible intervals overlapped zero. The spring eBird trend for Blue-winged Warbler was similar to the BBS trend in magnitude and precision, but the credible interval overlapped zero for the BBS trend. Golden-winged Warblers showed similar negative trends in eBird and BBS data, but fall eBird data showed a stable trend.

The two raptors, Bald Eagle and Peregrine Falcon, showed similar trends between eBird and BBS, and long-term trajectories matched the known pattern of a historical decline followed by a rebound after the use of DDT was banned.

DISCUSSION

Results of the models suggest that eBird data could play an important role in estimating population trajectories for species that are poorly represented in traditional and more-structured bird monitoring efforts. Similarly, the eBird database provides a unique opportunity to aggregate and use checklists from historic times, which could be used to model population trajectories prior to the advent of current long-term surveys and provide a broader context for interpreting more recent changes in population size. As with the CBC, eBird may not currently have sufficient data to model population change reliably for most species prior to circa 1970, which was evident in the large credible intervals around annual indices from the eBird models in early years. However, the eBird dataset is continuously growing and there exists a huge repository of historical checklists in the field notebooks of living and deceased bird-watchers. We suggest that with additional eBird checklists and enhanced statistical modeling techniques that account for known sources of bias in the data, it should be possible to derive improved estimates of historical changes in population trajectories for many species.

The positive correlations shown between seasons when comparing annual indices, trends, and residuals from trend models, suggest that models of eBird data reflect underlying population trajectories, because the datasets were discrete. Although credible intervals for annual indices became much wider further back in time, we suggest this is primarily due to the smaller sample sizes in those years. Because eBird was launched in 2002, all checklists prior to that year were effectively historical checklists that were recorded before eBird protocols were in place. The correlations between seasonal trends and trajectories and between eBird, BBS, and CBC dating back to 1970 were encouraging, suggesting that the methods used for incorporating historical lists were effective at extracting signal from noise. Because the eBird dataset is continuously growing (including historical checklists)

Table 7. Coefficients and *P* values for correlations between annual indices from eBird models and annual indices from BBS data between 1970 and 2015, in descending order by strength of correlation between spring eBird models and BBS. Correlations between BBS and spring, fall, and winter eBird data are in separate columns. See Table 1 for scientific species names.

	Spring		Fall		Winter	
Species	*r*	*P*	*r*	*P*	*r*	*P*
Bald Eagle	0.952	< 0.0001	0.963	< 0.0001	0.892	< 0.0001
Evening Grosbeak	0.863	< 0.0001	0.819	< 0.0001	0.845	< 0.0001
Northern Parula	0.806	< 0.0001	0.666	< 0.0001		
Rusty Blackbird	0.797	< 0.0001	0.641	< 0.0001	0.743	< 0.0001
Cape May Warbler	0.779	< 0.0001	0.807	< 0.0001		
Golden-winged Warbler	0.774	< 0.0001	0.092	0.5482		
Peregrine Falcon	0.745	< 0.0001	0.700	< 0.0001	0.768	< 0.0001
Canada Warbler	0.702	< 0.0001	0.787	< 0.0001		
Tennessee Warbler	0.675	< 0.0001	0.355	0.0153		
Olive-sided Flycatcher	0.583	< 0.0001	0.578	< 0.0001		
Least Flycatcher	0.580	< 0.0001	-0.669	< 0.0001		
American Tree Sparrow	0.558	0.0003	0.357	0.0277	0.544	0.0004
Le Conte's Sparrow	0.555	0.0001	0.509	0.0005	0.666	< 0.0001
Wilson's Warbler	0.452	0.0016	0.590	< 0.0001		
Pine Siskin	0.411	0.0045	0.405	0.0052	0.492	0.0005
Connecticut Warbler	0.323	0.0303	0.433	0.0029		
Blue-winged Warbler	0.311	0.0352	0.269	0.0706		
Gray-cheeked Thrush	0.296	0.0638	-0.003	0.9854		
Black-throated Blue Warbler	0.223	0.1365	0.047	0.7564		
Bay-breasted Warbler	0.131	0.3850	0.177	0.2402		
Blackpoll Warbler	0.115	0.4452	-0.278	0.0611		
Yellow-bellied Flycatcher	0.054	0.7212	0.000	0.9981		
White-crowned Sparrow	-0.029	0.8478	-0.298	0.0441	-0.083	0.5821
Common Redpoll	-0.118	0.5139	0.074	0.6817	0.080	0.6593
Magnolia Warbler	-0.121	0.4245	-0.063	0.6770		

estimating historical population trajectories using these (or other) methods should only improve in the future.

Although results indicated positive relationships between seasons for most species, several species showed disagreement in sign or magnitude of trend. Focusing on years since 1970 when data were plentiful, the following seven species showed noteworthy disagreement in seasonal population trajectories: Least Flycatcher, Golden-winged Warbler, Blackpoll Warbler (*Setophaga striata*), Tennessee Warbler, LeConte's Sparrow (*Ammodramus leconteii*), Evening Grosbeak, and Common Redpoll (*Acanthis flammea*). In general, when seasonal trajectories differ we believe that spring eBird trajectories are likely more representative of the population than fall trajectories for several reasons: the spring eBird dataset contains more checklists than the other seasons, birds are more likely to produce diagnostic vocalizations in spring than in other seasons, plumages of many species are more distinctive in spring, and effects of juveniles and winter mortality have been moderated. Discrepancies for three of these species (Least Flycatcher, Tennessee Warbler, and Blackpoll Warbler) may stem from difficulties in fall identification. One is an *Empidonax* flycatcher, a group well-known for being difficult to identify in fall when they seldom vocalize. The two warbler species are among several species often referred to as confusing fall warblers because they are relatively nondescript and similar to one another. Many fall *Empidonax* and confusing fall warblers are left unidentified, but advances in identification of these species may have led to increased reporting rates over time, which would introduce bias. For Golden-winged Warblers, both spring and fall trajectories showed clear but different patterns, with fall indices showing a peak in frequency in the 1990s that was not present in the spring indices. This peak may have an unknown underlying biological explanation. Evening Grosbeaks differed seasonally in the magnitude of the trend estimates, but all seasons showed steep declines. For Common Redpolls and LeConte's Sparrows, trends agreed between two of the seasons but not the third. Common Redpolls are irruptive finches, and when irruptions occur are most likely to arrive in the northeastern U.S. in late November or December. In most years, the fall season as defined for this study would not likely overlap with the irruption from the Arctic.

Correlations between area defoliated by spruce budworm in the boreal forest and annual indices from eBird data for bird species that respond to spruce budworm outbreaks also suggest that modeling historical data is providing meaningful information on population change. Peaks of occurrence for the spruce budworm specialists largely corresponded to spruce budworm outbreaks, meaning that the models successfully captured population trajectories prior to and after 1970. Additionally, the three warbler species associated with spruce budworm showed recent increases in annual indices that coincide with the current outbreak of spruce budworm. Although peaks in occurrence of these species do not all exactly match the peaks in defoliation, we think this could have a biological explanation considering that the defoliation statistic is summed across the entire boreal forest. Regional peaks in defoliation differed by up to a decade, and so overlap with the extent of each species' breeding range varied. An in-depth analysis of these differences may be warranted, but was beyond the scope of this study. Several of our other focal species, i.e., Yellow-bellied

Flycatcher (*Empidonax flaviventris*), Blackpoll Warbler, and Canada Warbler, have shown positive responses to spruce budworm in some studies but not in others (Patten and Burger 1998, Venier et al. 2009). In this study, Canada Warbler trajectories from both spring and fall were moderately correlated with spruce budworm indices, but trajectories for Yellow-bellied Flycatcher and Blackpoll Warbler were not. Although many of the other focal species also showed positive correlations to spruce budworm defoliation, this could be expected for several reasons. Venier et al. 2009 noted an overall increase of territories across species during a spruce budworm outbreak, even after data from the specialist species were removed. This may be reflected in trajectories of some of the other boreal species. However, given that data from before 1970 were less influential because of the year bins, we think the long-term decline in defoliated area since 1970 might correlate well with any species that showed similar declines during that same time frame, and could explain why species that breed outside of the boreal forest were correlated with spruce budworm indices. Similarly, species that showed positive trajectories since 1970 such as Bald Eagle, Peregrine Falcon, Northern Parula, White-crowned Sparrow, and the fall model for Least Flycatcher, were all negatively correlated with the spruce budworm data. Although any species with similar declines since 1970 may be somewhat correlated with area defoliated by spruce budworm, the fact that the four species of spruce budworm specialists showed the highest correlations out of the species analyzed supports the efficacy of modeling populations using eBird data.

The annual indices and trends generated using models of eBird data agreed surprisingly well with those from the BBS, considering that many of the species have ranges that only overlap BBS coverage at their extremities. Species with higher reliability scores based on BBS, CBC, or other survey data by ECCC 2014*a* showed trends more similar to those in eBird than did species with low reliability (Fig. 5). Although there was no apparent systematic bias between eBird data and BBS data, eBird data produced more negative trends than CBC data.

The eBird dataset provides an opportunity to assess the status of boreal species with low or deficient trend reliability from BBS and CBC from a new perspective. Of the 10 species analyzed with low or deficient trend reliability, 8 have migratory routes that pass through areas with high eBird coverage, which highlights the utility of the eBird dataset. Some of these species, such as Gray-cheeked Thrush (*Catharus minimus*) and Lapland Longspur (*Calcarius lapponicus*), showed long-term declines in frequency of occurrence that have not been detected by other surveys. For other species, such as Blackpoll Warbler and Common Redpoll, trajectories from eBird data were more positive than those from BBS, and did not exhibit the steep declines shown by the latter. This could have important management implications. For instance, based on BBS data, Blackpoll Warbler was recently highlighted as a common species in steep decline by the Partners in Flight Landbird Conservation Plan 2016 Revision (Rosenberg et al. 2016), but long-term trajectories from eBird appeared to be stable. The BBS covers a small fraction of the breeding range of Blackpoll Warblers, whereas the majority of the population passes through areas of the eastern U.S. with high eBird coverage, suggesting the eBird trend may be more representative of the population. Thus, the use of eBird data could play an important role in assessing populations of boreal and Arctic breeding species, especially for those species that migrate through eastern North America or along the Pacific Coast where eBird coverage is the highest. For some species though, the utility of eBird data to monitor populations remains limited. For one species in this study, Smith's Longspur, low detection rates combined with sparse eBird coverage within its range yielded small annual sample sizes and poor precision in trend estimates. The species was still included in the analyses to demonstrate the lower limits for sample sizes using this modeling technique. Additionally, very little is known about population trajectories for this species based on other surveys so the eBird data could provide the best estimates to date.

The large, nearly range-wide scale of these models during migration allowed for aggregation of checklists from a broad geographic area, which provided the sample sizes necessary to model trajectories in historic times. The 40-kilometer square grid cell that was used to group checklists geographically helped reduce bias from uneven geographic coverage, and the vast amount of data in recent years yielded estimates of frequency of occurrence for these cells. The shortcoming of this method, is that annual indices from different years may be weighted toward different regions, depending on where the checklists originated. This method essentially assumes that there are not regional differences in population trajectories for each species. Currently, there are not enough historic lists in eBird to model regional trends within a global model, though there may be several regions with enough data to model trajectories independently. The long-term trajectories we presented are largely influenced by eBird data from the eastern U.S., primarily along the east coast and in the Great Lakes area. For species whose populations primarily pass through these areas during migration, the models presented likely provide a reasonable estimate of change in frequency of occurrence. For species that pass through or winter in the center of the continent, the trajectories would be biased toward the eastern portion of their range. For the few species analyzed whose ranges reach the Pacific coast, the results would also be biased toward data from California, where there is a high density of historic lists.

The results of our indirect assessments of long-term population trajectories generated by eBird data matched our predictions: population trajectories largely agreed between seasons, Bald Eagle and Peregrine Falcon trajectories mirrored known patterns, and annual indices of species associated with spruce budworm outbreaks were strongly correlated to that of area defoliated by spruce budworm. Additionally, correlations between eBird, BBS, and CBC trajectories were positive despite differences in sampling methodology, statistical analysis, and geographic coverage, suggesting that our methodology was successful at extracting signal from noise in the eBird dataset. More work is needed to determine the reliability and precision of trajectories estimated from eBird data, and to clarify the nature of the relationship between frequency of occurrence on eBird checklists and population size for various species.

The endeavor to model population trajectories prior to 1970 was hampered by the limited number of checklists in those years, but efforts to locate and enter historic lists into eBird could remedy this. We did not attempt to assess the annual sample sizes of checklists that would be necessary to produce reliable estimates.

This would not be straightforward considering that the information content of each checklist is so variable based on the amount of effort and number of species detected, and detection rates for each species are different. However, it was evident that the credible intervals around annual indices in the eBird models become much wider before 1970 for most species, so sample sizes used for 1970s in this study may serve as a guideline for the minimum at a continental scale. Regional studies may require far fewer checklists to overcome geographic bias. We believe that efforts to boost historical sample sizes are critical because examination of long-term population trajectories that date back to before 1970 is essential for assessing the status of some species. For example, the spruce budworm specialists all show long-term declines since 1970, but 1970 coincides with the peak of the last spruce budworm outbreak. Only data prior to 1970 address the long-term status of these species, and of other species that have population cycles with large amplitudes. The strength of the relationships between seasons and datasets post 1970 imply that the methodology for modeling trajectories from historic eBird checklists is sound, and that a concentrated effort to increase sample sizes from historic times by an order of magnitude would provide important context for understanding current population changes.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1671

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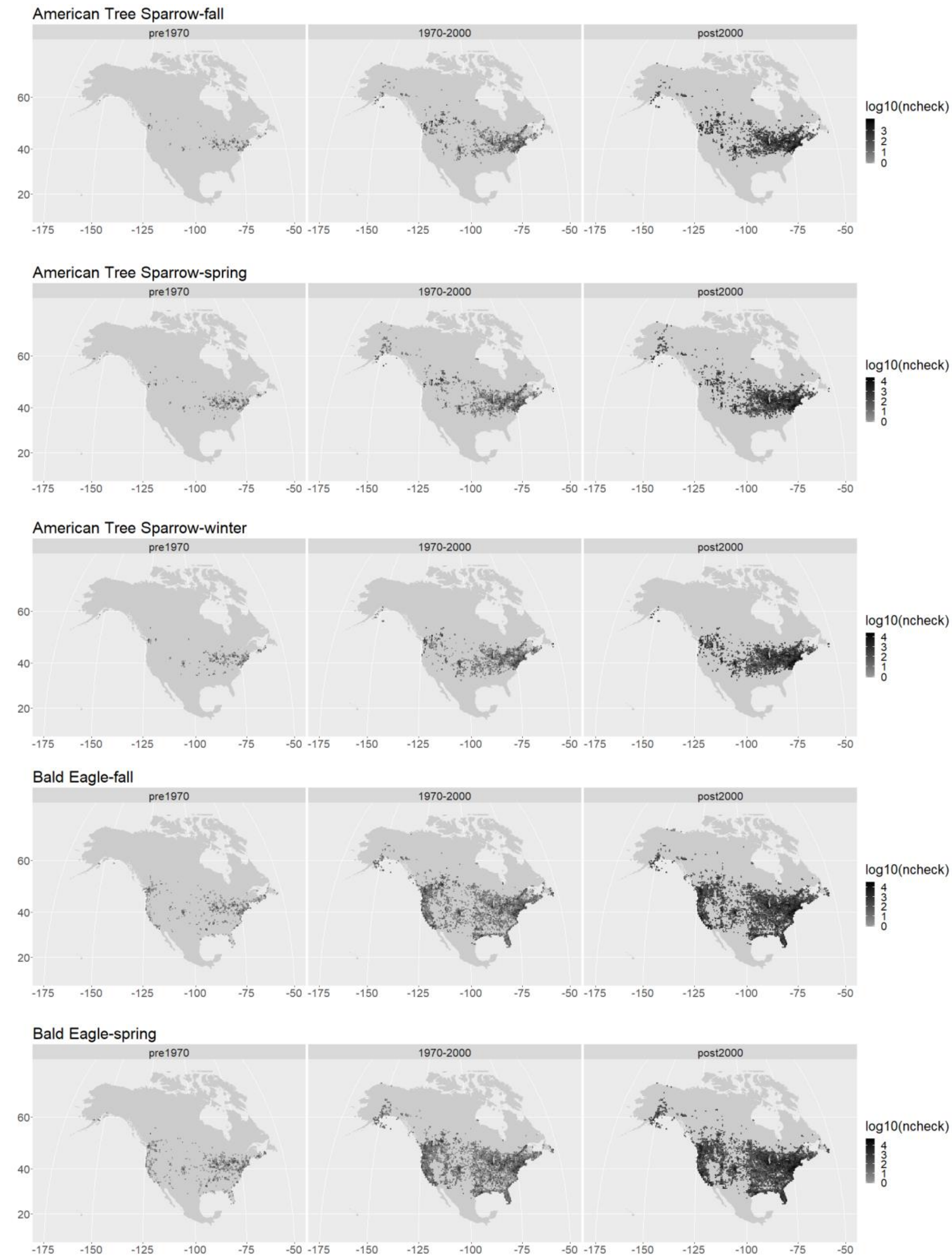
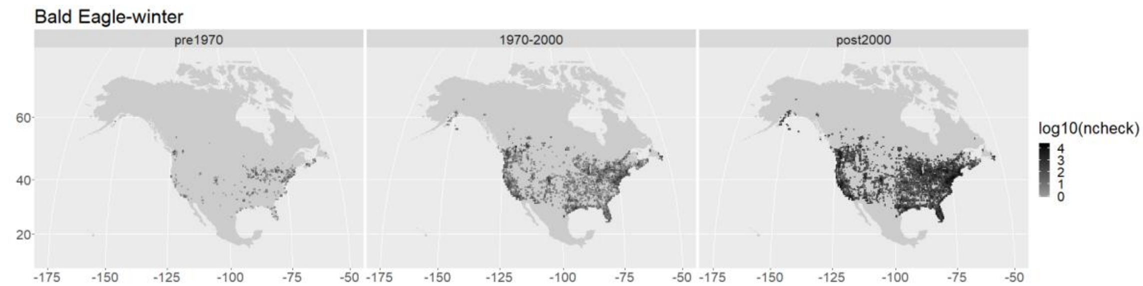
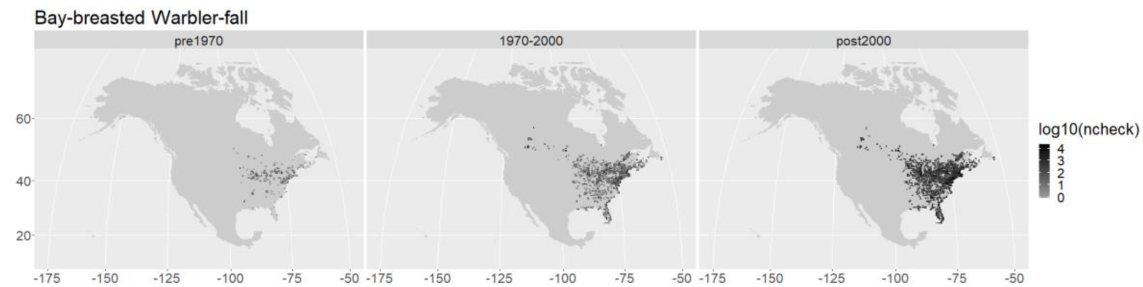
Appendix 1. Table depicting how each specialized protocol type in eBird was reclassified as one of the standard protocol types, and which protocol types were removed from the analysis.

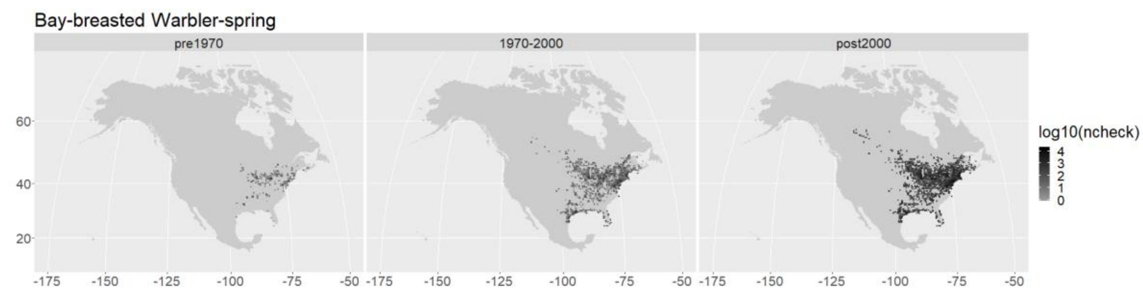
New Protocol	Specialized Protocol
Traveling Count	Historical
	Exhaustive Area Count
	Audubon NWR Protocol
	Traveling-Property Specific
	Great Texas Birding Classic
	Texas Shorebird Survey
	eBird California - YellowBilledMagpie Traveling
	eBird Vermont - LoonWatch
	eBird Caribbean - CWC Area Search
	eBird--Heron Area Count
	eBird--Rusty Blackbird Blitz
	IBA Canada
	eBird Random Location Count (with km)
Stationary Count	eBird Caribbean - CWC Stationary Count
	eBird--Heron Stationary Count
	eBird Random Location Count (w/o km)
	My Yard eBird - Standardized Yard Count
	eBird My Yard Count
Incidental	eBird California - YellowBilledMagpie General
Removed	GCBO - GCBO Banding Protocol
	RMBO Early spring Waterbird Count
	eBird - Oiled Birds
	TNC California Waterbird Count
	Birds 'n' Bogs Survey
	California Brown Pelican Survey
	RMBO Early Winter Waterbird Count
	Nocturnal Flight Call
	eBird Pelagic Protocol
	PriMig - Pri Mig Banding Protocol

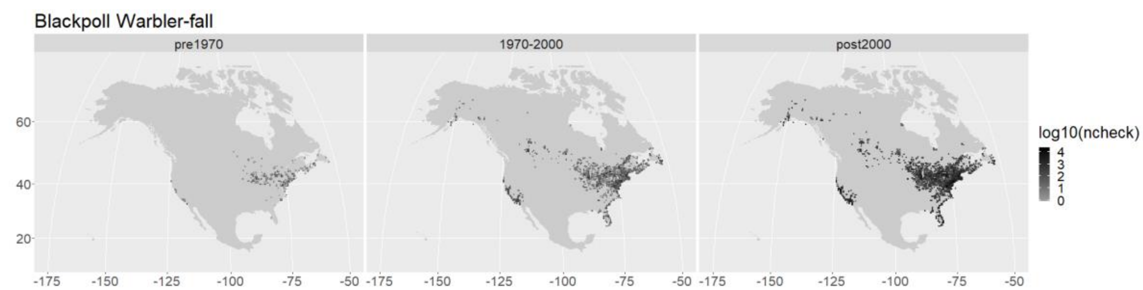
Appendix 2. Maps showing the geographic density of checklists (ncheck) in each 40 x 40 km grid cell for each species and season over time.

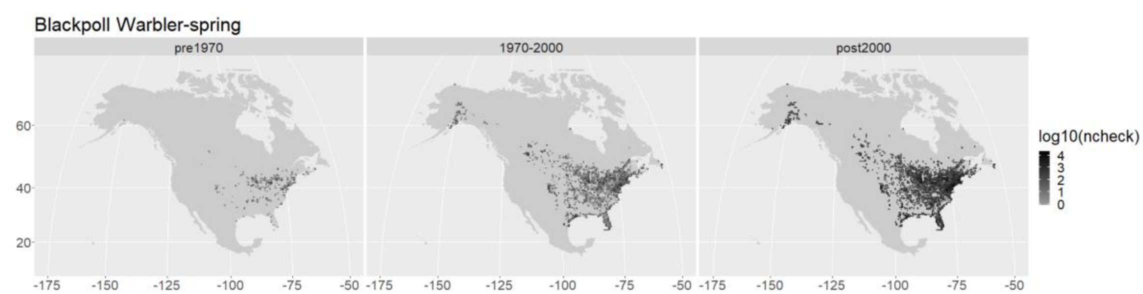



Bald Eagle-winter
pre1970
1970-2000
post2000
60
40
20
-175 -150 -125 -100 -75 -50
log10(ncheck)
4
3
2
1
0

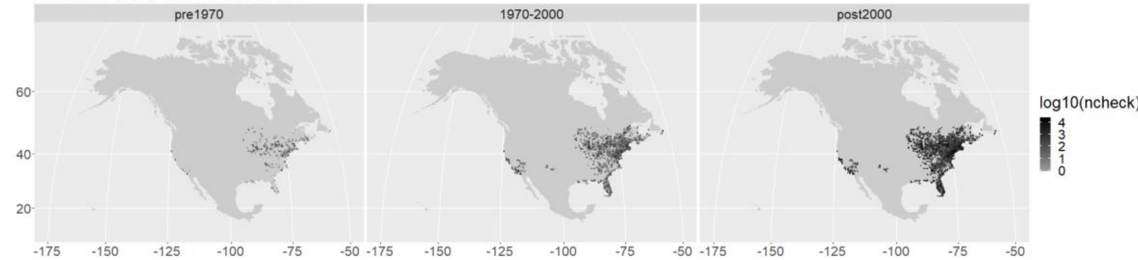

Bay-breasted Warbler-fall
pre1970
1970-2000
post2000
60
40
20
-175 -150 -125 -100 -75 -50
log10(ncheck)
4
3
2
1
0


Bay-breasted Warbler-spring
pre1970
1970-2000
post2000
60
40
20
-175 -150 -125 -100 -75 -50
log10(ncheck)
4
3
2
1
0

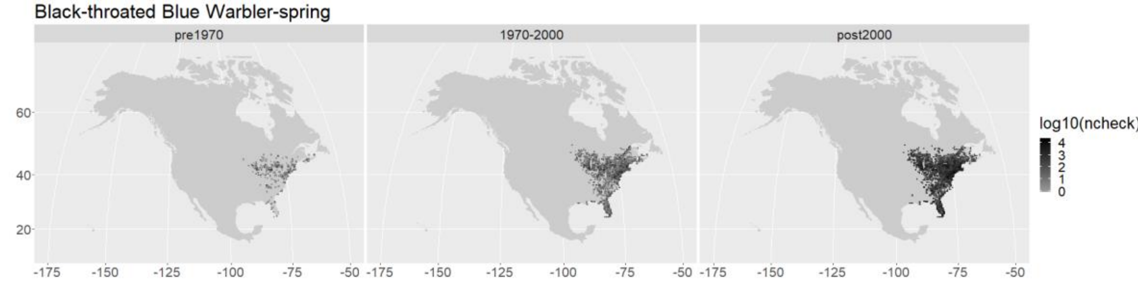

Blackpoll Warbler-fall
pre1970
1970-2000
post2000
60
40
20
-175 -150 -125 -100 -75 -50
log10(ncheck)
4
3
2
1
0


Blackpoll Warbler-spring
pre1970
1970-2000
post2000
60
40
20
-175 -150 -125 -100 -75 -50
log10(ncheck)
4
3
2
1
0

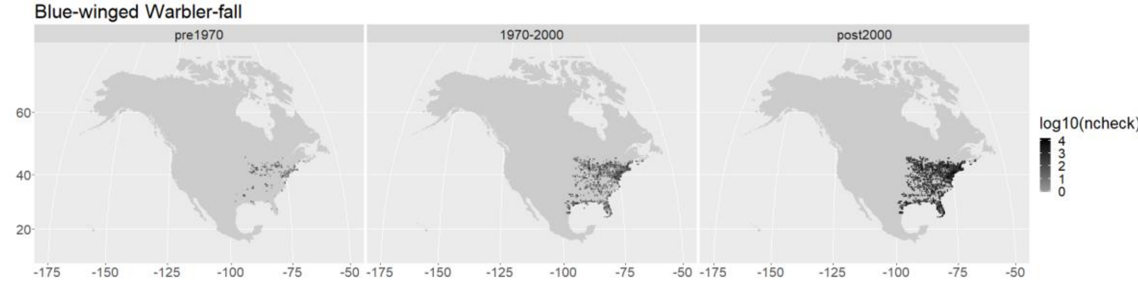
Black-throated Blue Warbler-fall



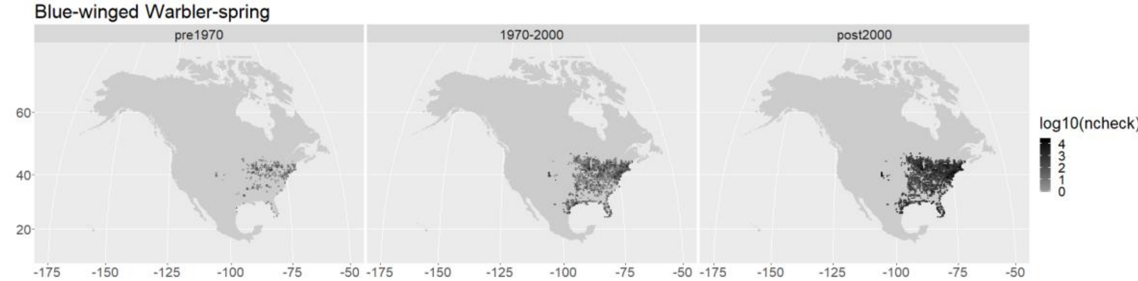
Black-throated Blue Warbler-spring



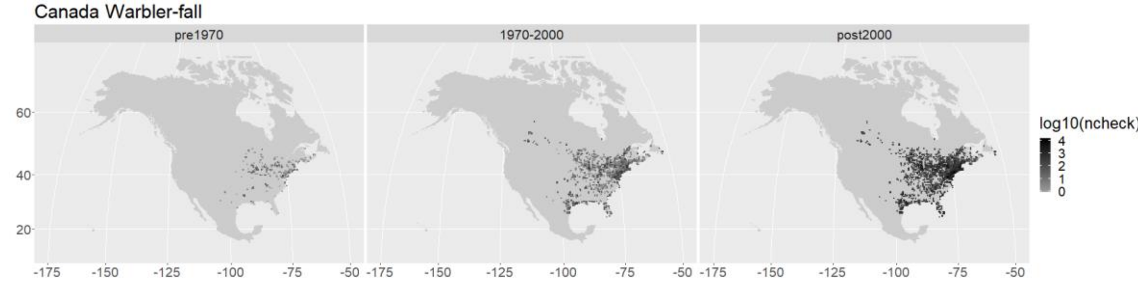
Blue-winged Warbler-fall

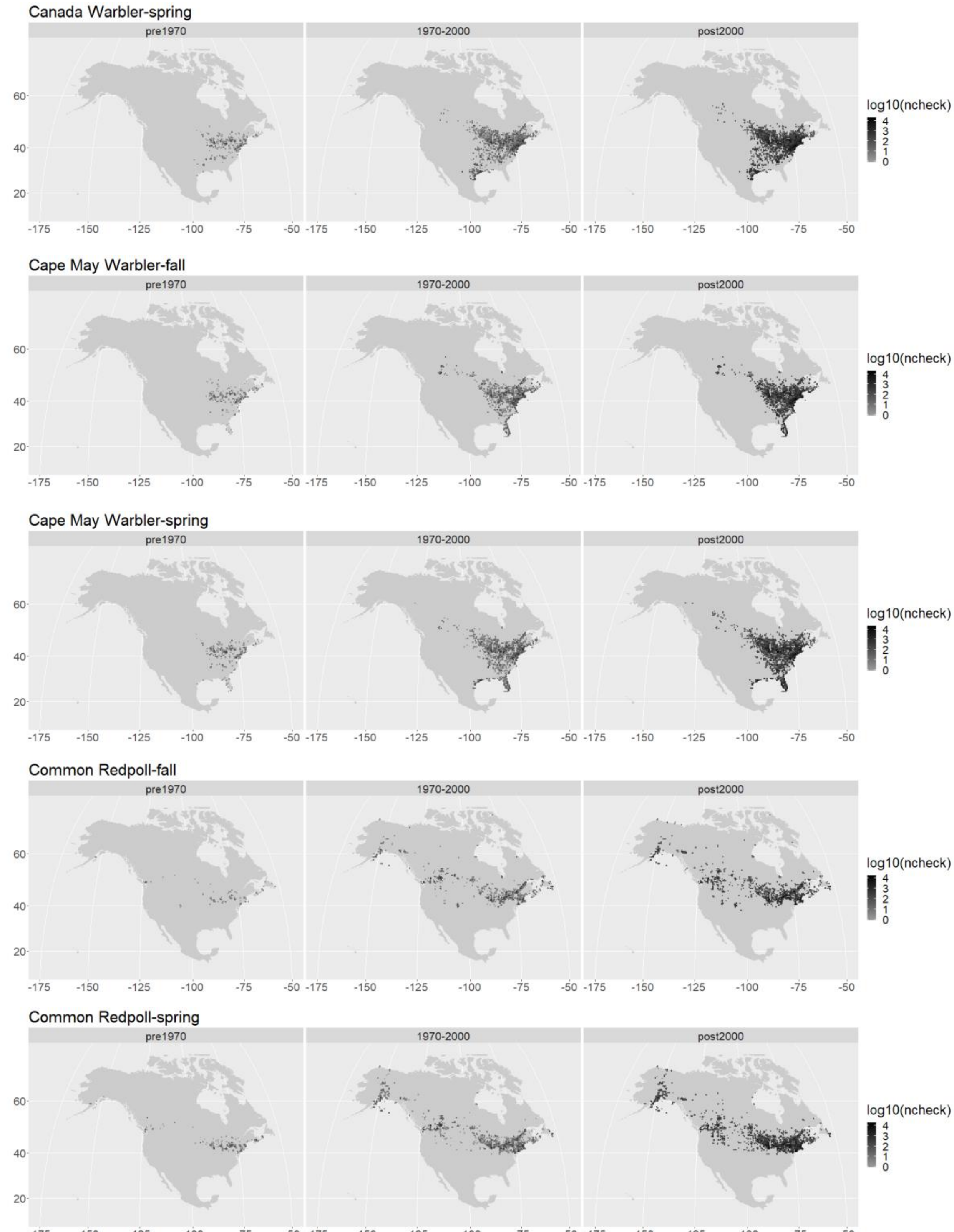


Blue-winged Warbler-spring



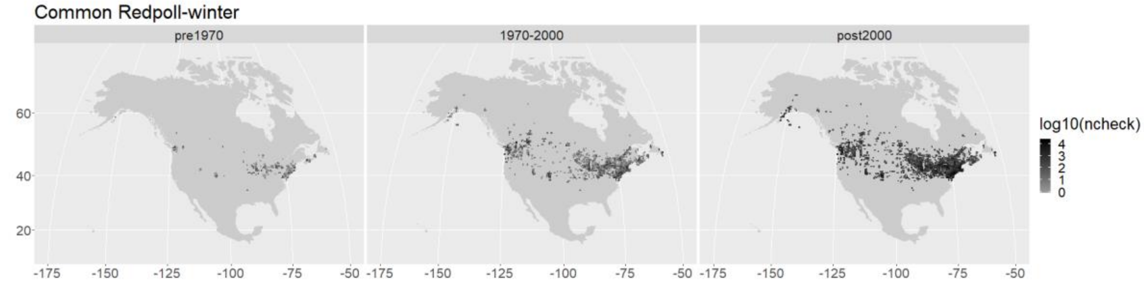
Canada Warbler-fall



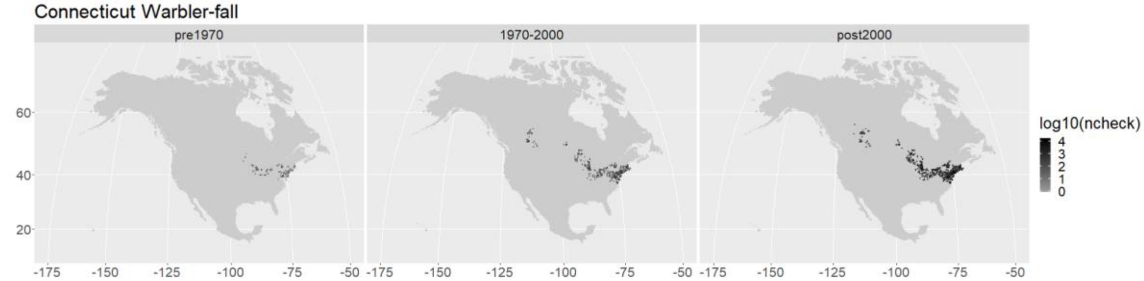


Canada Warbler-spring
Cape May Warbler-fall
Cape May Warbler-spring
Common Redpoll-fall
Common Redpoll-spring
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175
-150
-125
-100
-75
-50

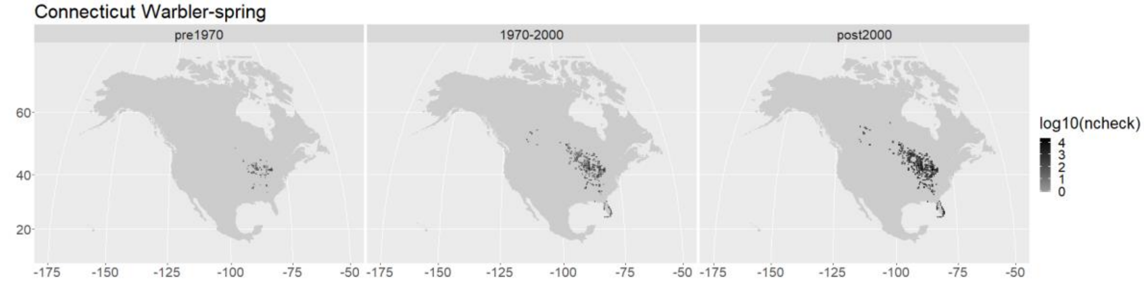
Common Redpoll-winter



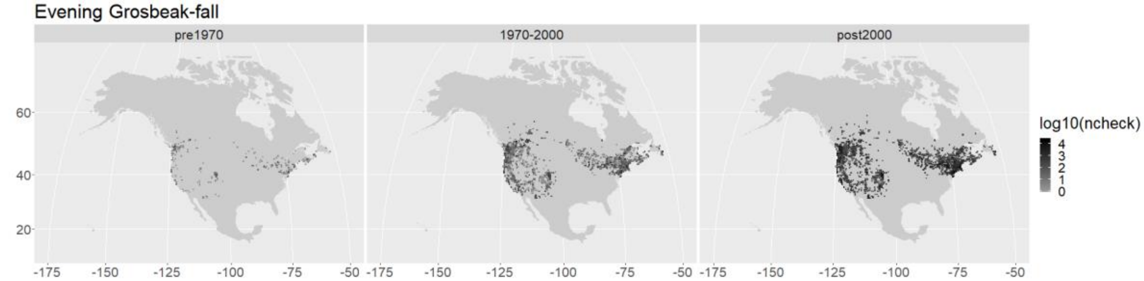
Connecticut Warbler-fall



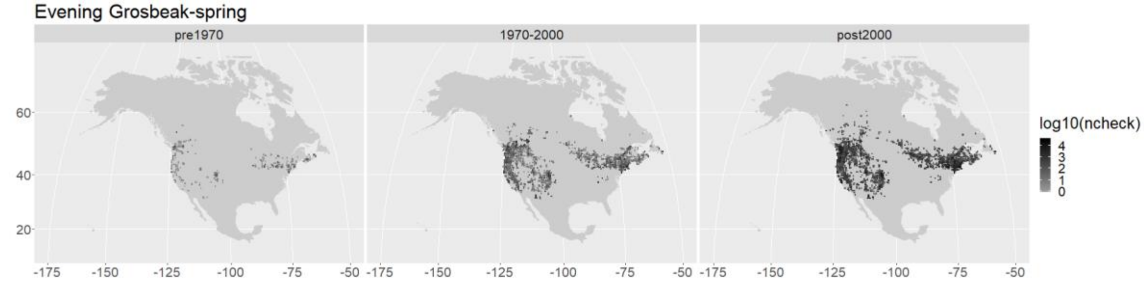
Connecticut Warbler-spring



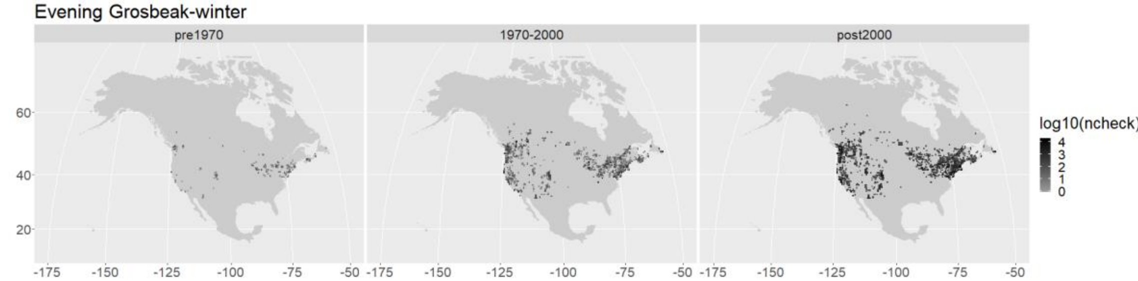
Evening Grosbeak-fall



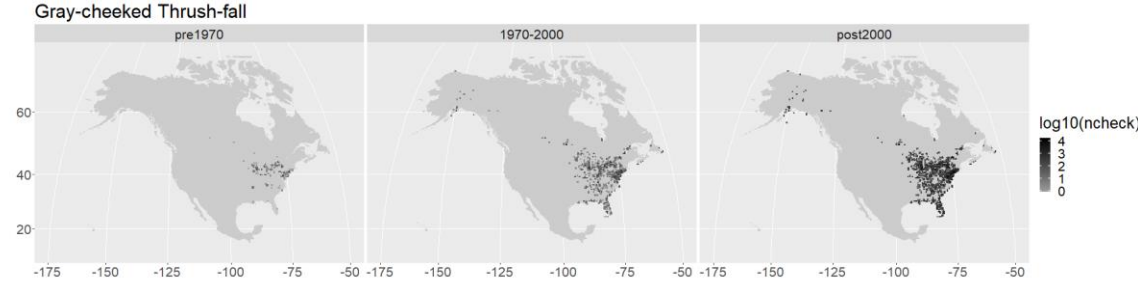
Evening Grosbeak-spring



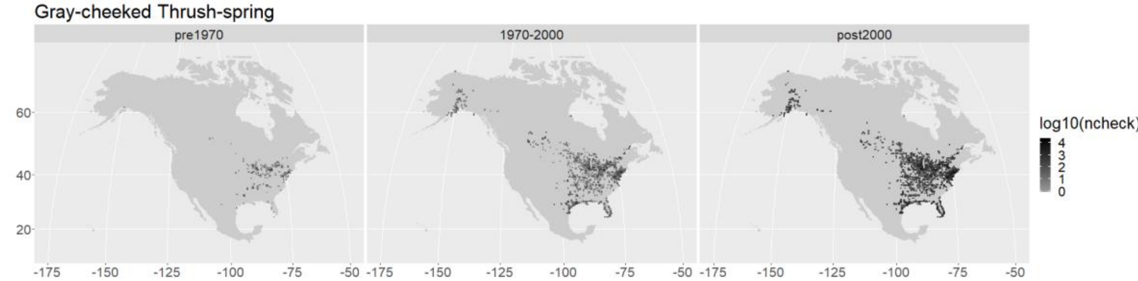
Evening Grosbeak-winter



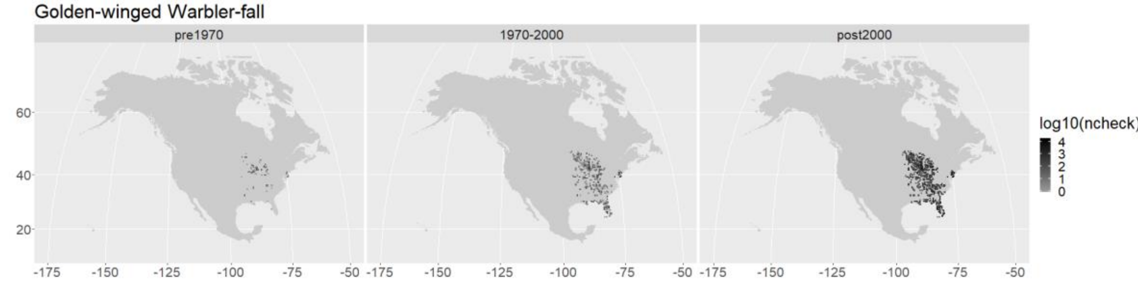
Gray-cheeked Thrush-fall



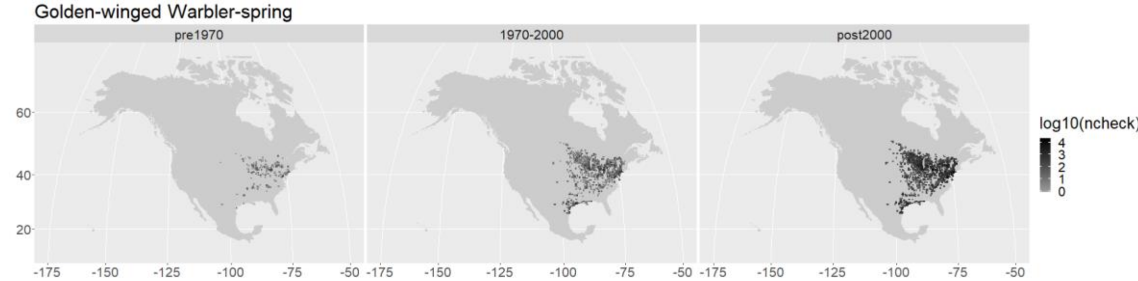
Gray-cheeked Thrush-spring

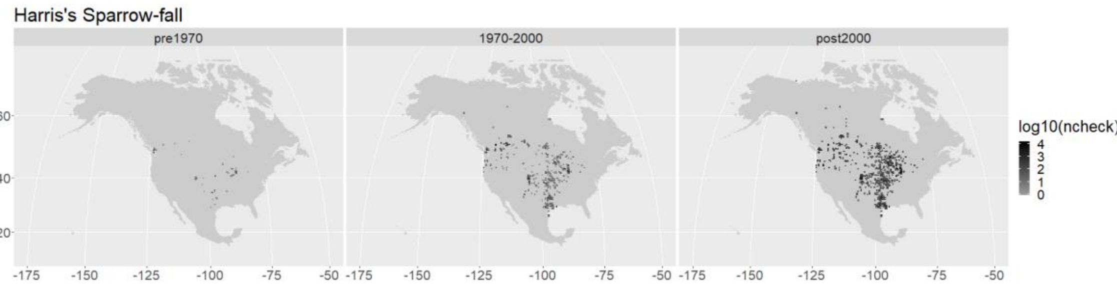


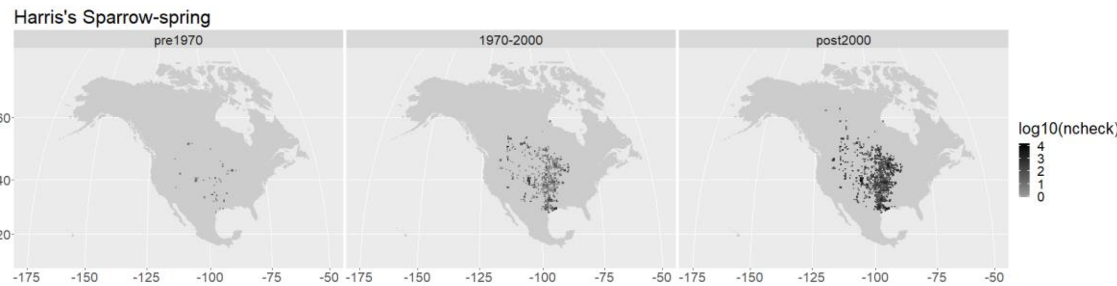
Golden-winged Warbler-fall

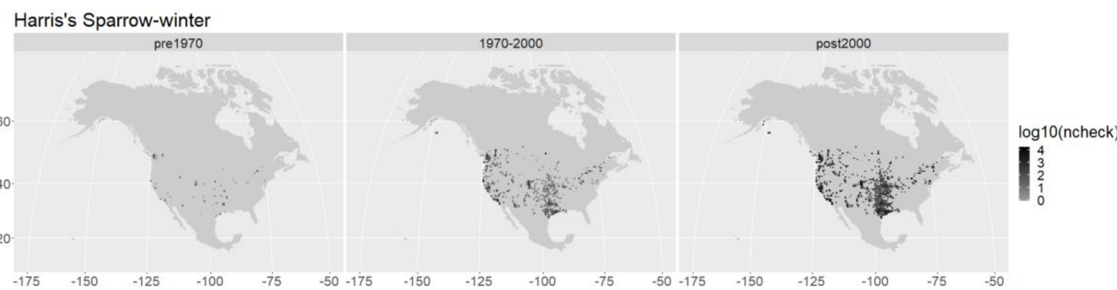


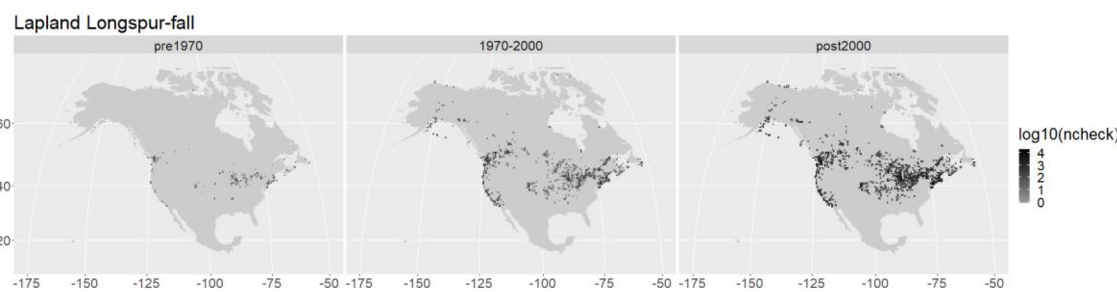
Golden-winged Warbler-spring

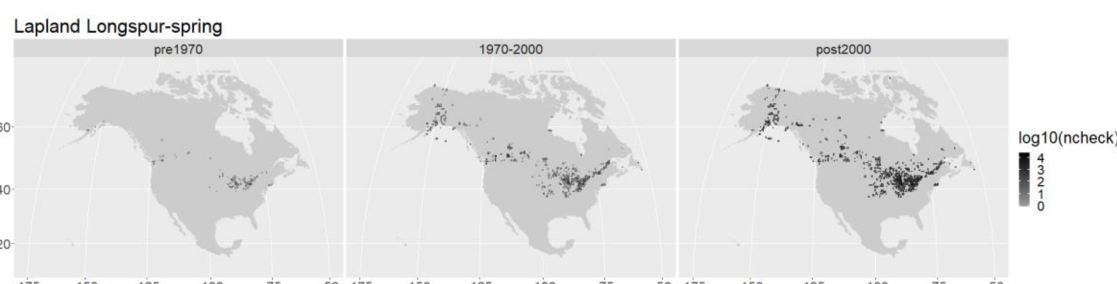



Harris's Sparrow-fall
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50

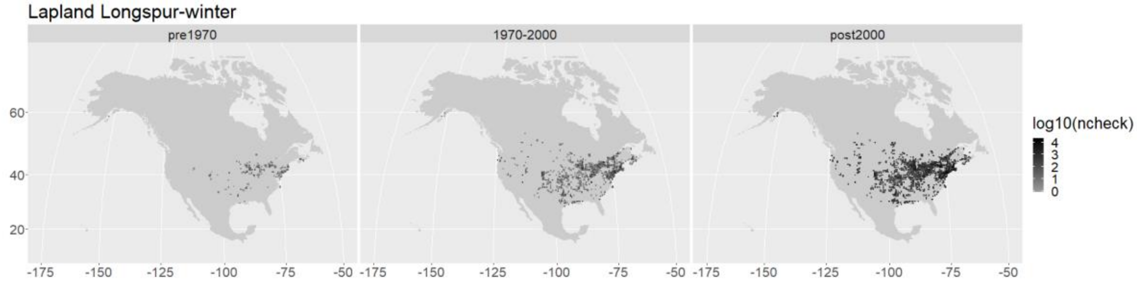

Harris's Sparrow-spring
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50


Harris's Sparrow-winter
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50

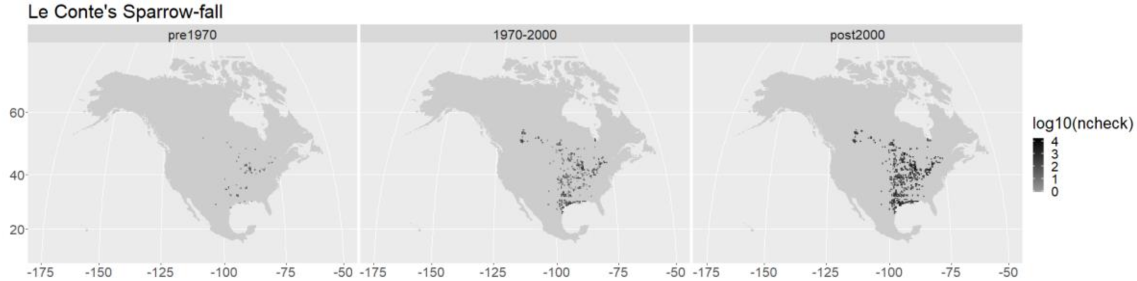

Lapland Longspur-fall
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50


Lapland Longspur-spring
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50

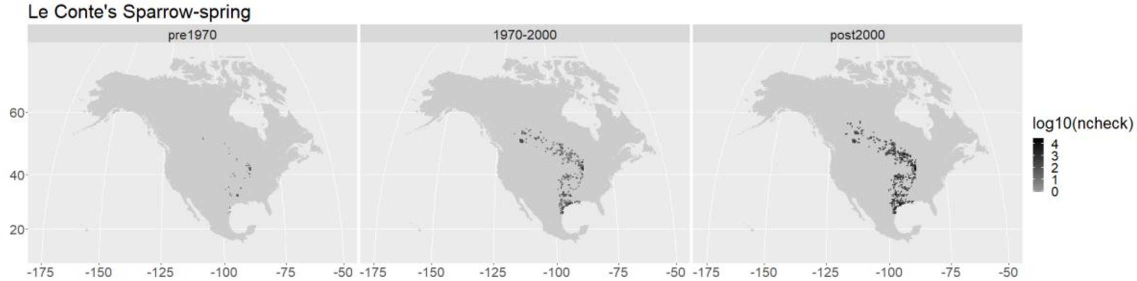
Lapland Longspur-winter



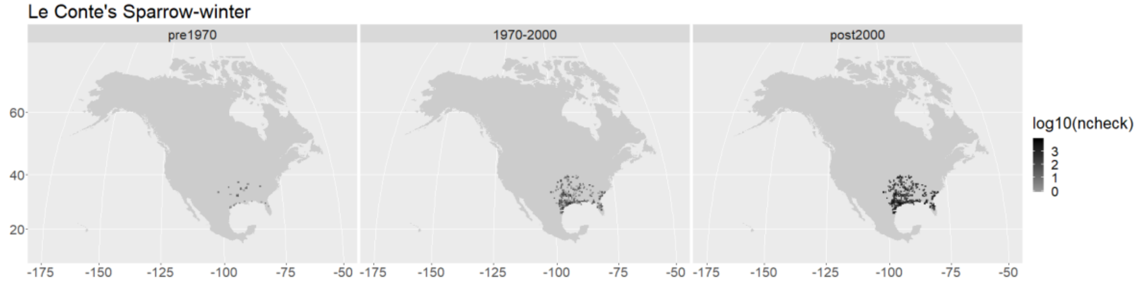
Le Conte's Sparrow-fall



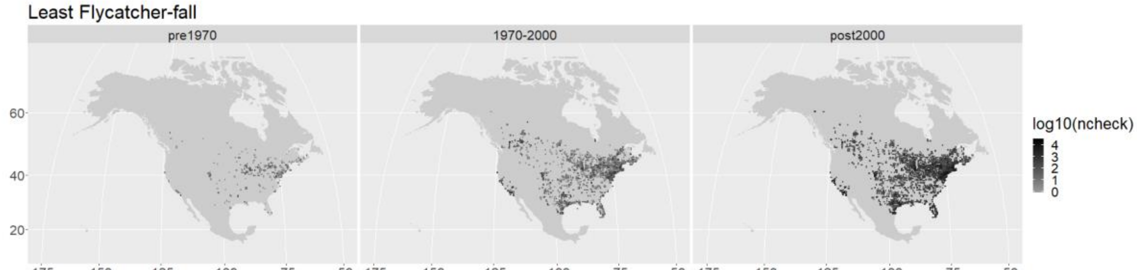
Le Conte's Sparrow-spring



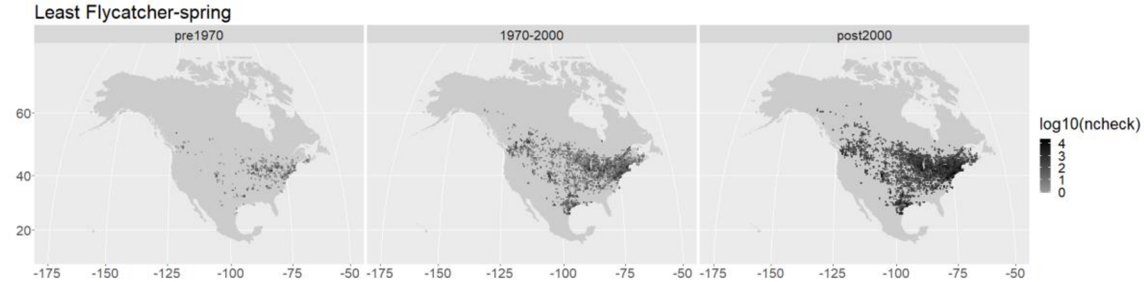
Le Conte's Sparrow-winter



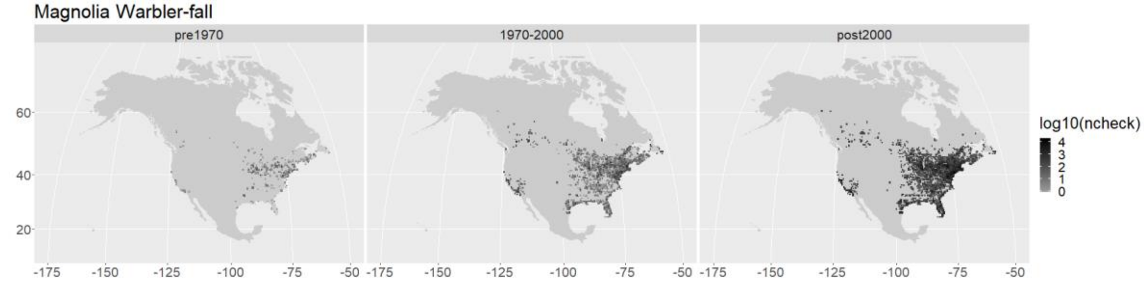
Least Flycatcher-fall



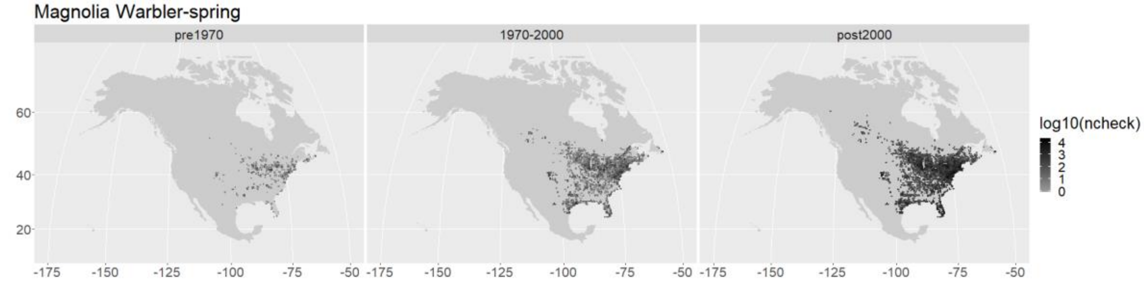
Least Flycatcher-spring



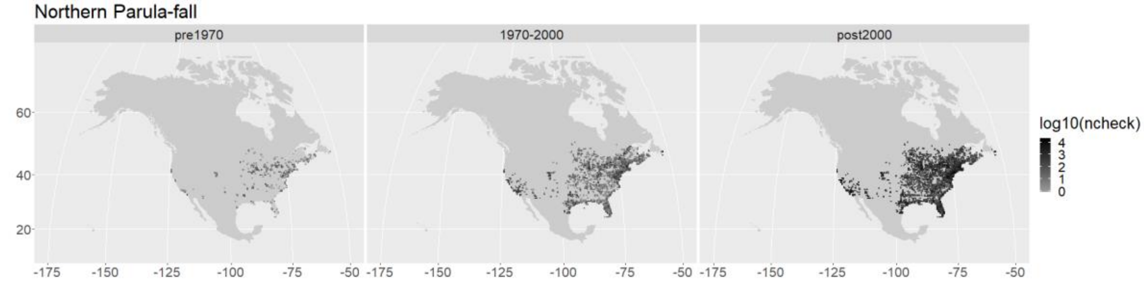
Magnolia Warbler-fall



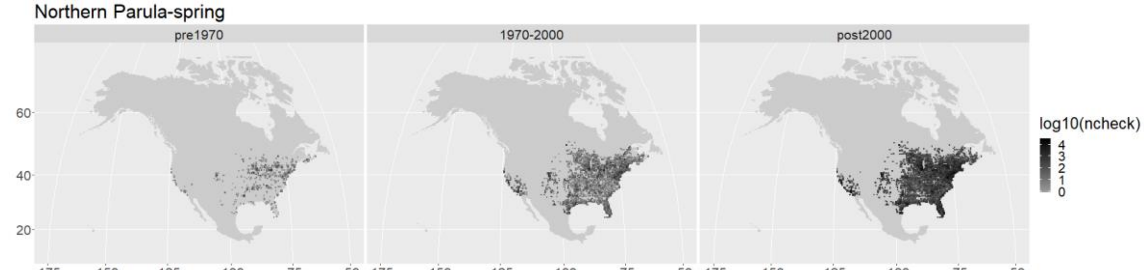
Magnolia Warbler-spring

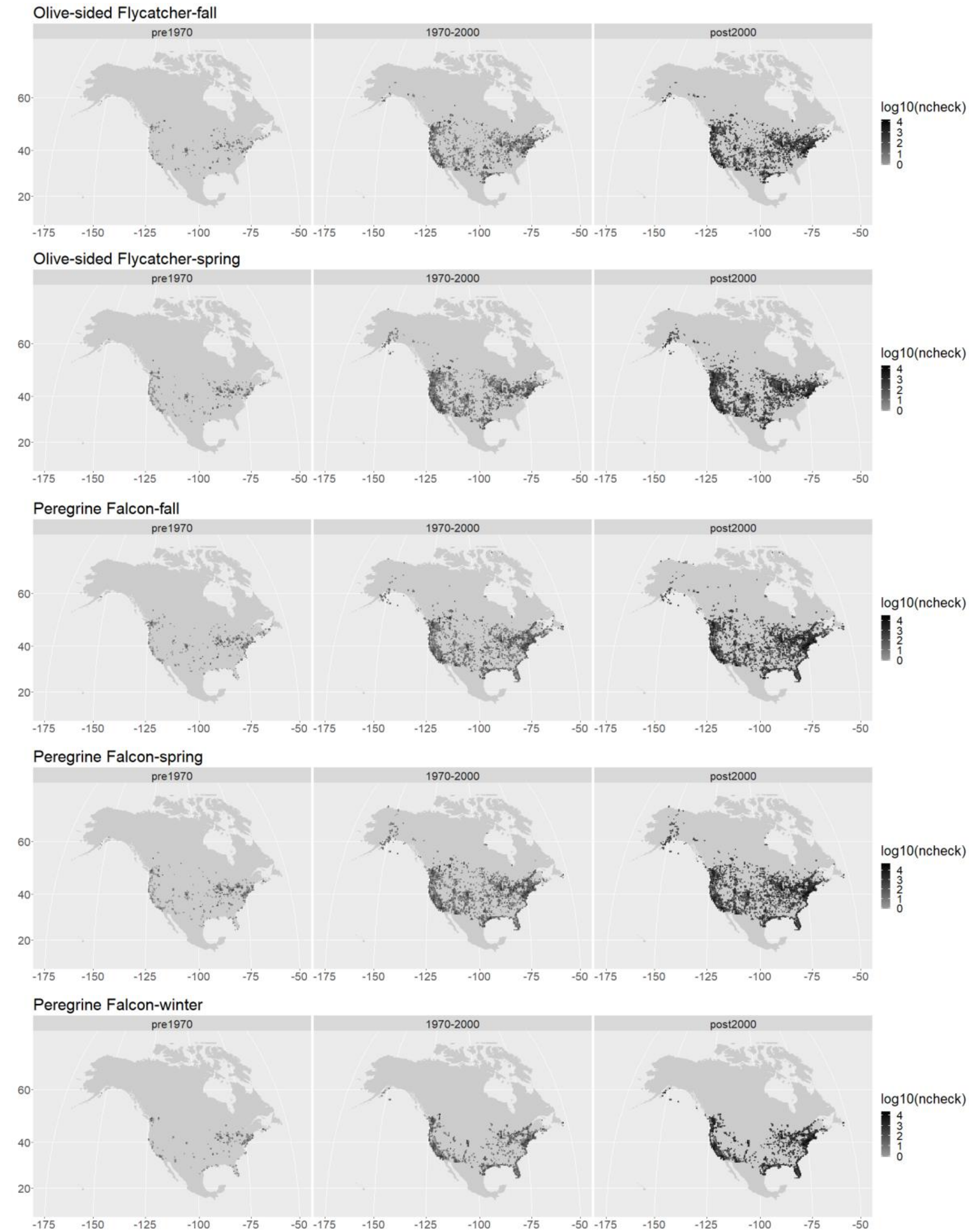


Northern Parula-fall

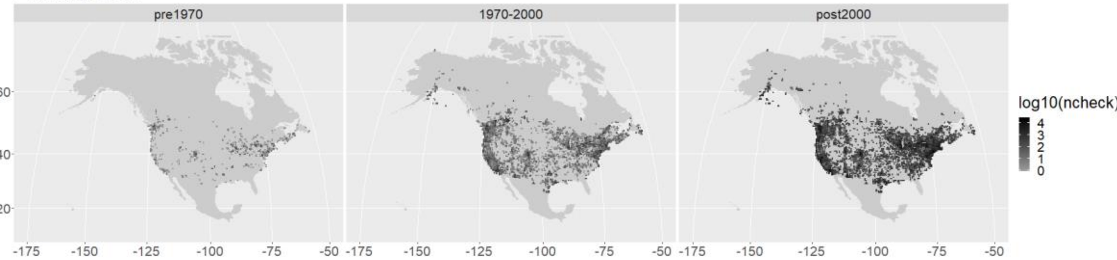


Northern Parula-spring

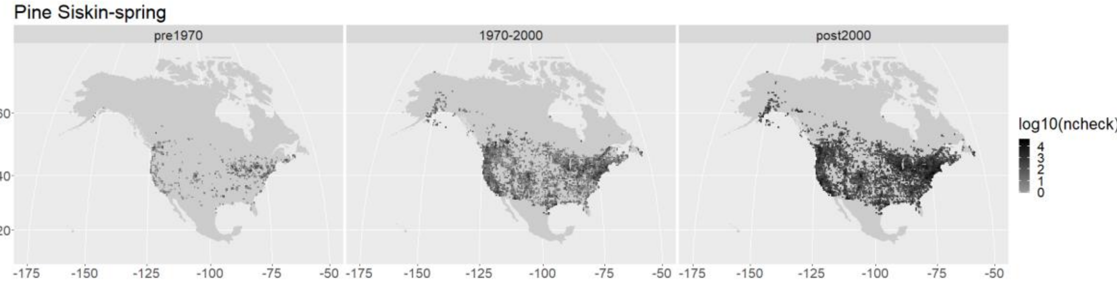



Olive-sided Flycatcher-fall
pre1970
1970-2000
post2000
log10(ncheck)
Olive-sided Flycatcher-spring
Peregrine Falcon-fall
Peregrine Falcon-spring
Peregrine Falcon-winter
60
40
20
-175 -150 -125 -100 -75 -50
4
3
2
1
0

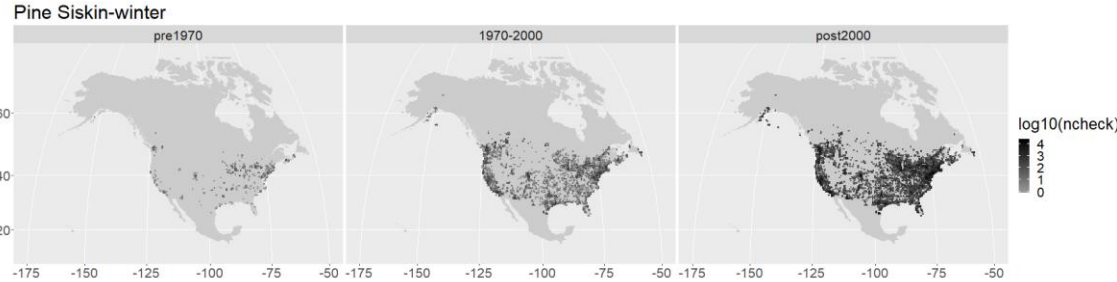
Pine Siskin-fall



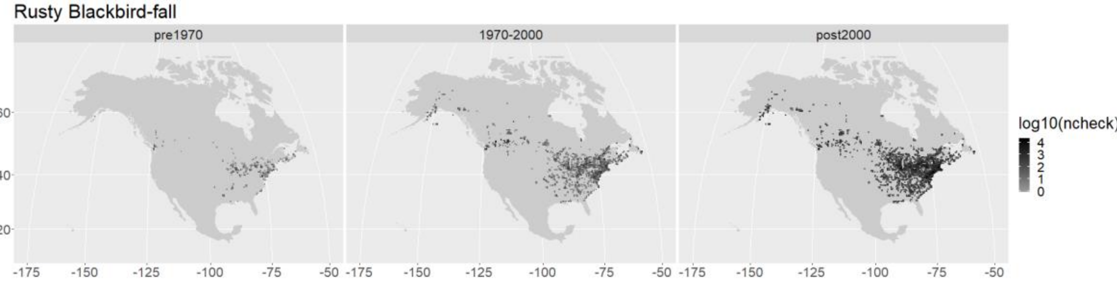
Pine Siskin-spring



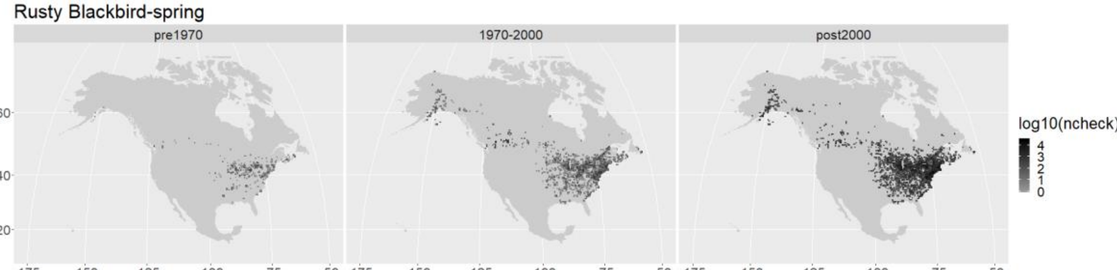
Pine Siskin-winter

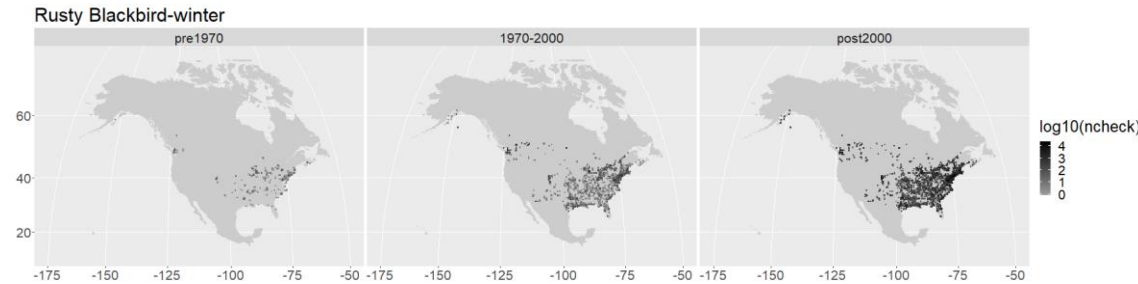


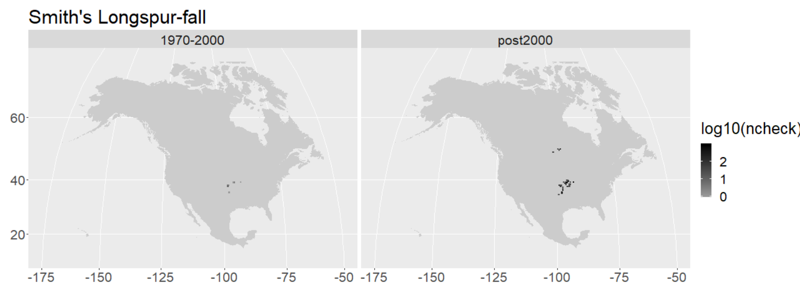
Rusty Blackbird-fall



Rusty Blackbird-spring




Rusty Blackbird-winter
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0


Smith's Longspur-fall
1970-2000
post2000
log10(ncheck)
2
1
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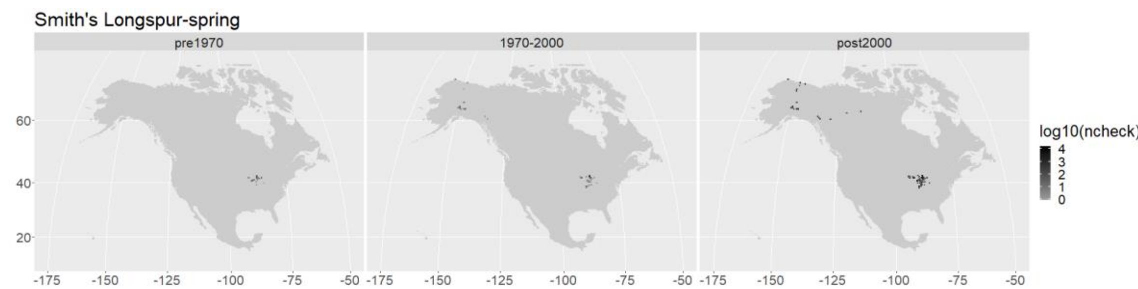
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pre1970
1970-2000
post2000
log10(ncheck)
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3
2
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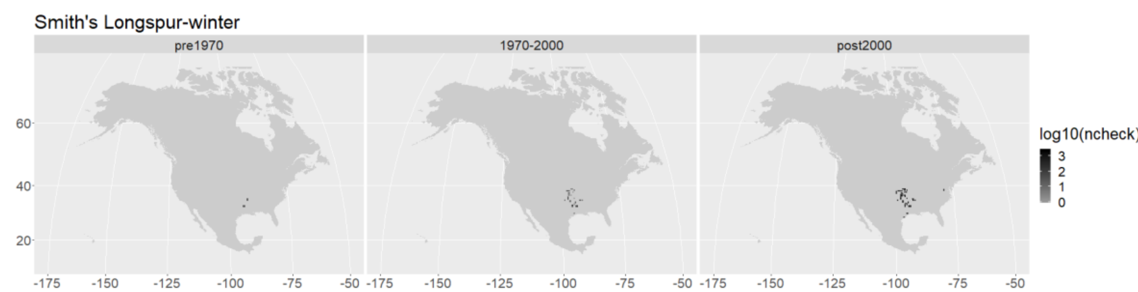
Smith's Longspur-winter
pre1970
1970-2000
post2000
log10(ncheck)
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2
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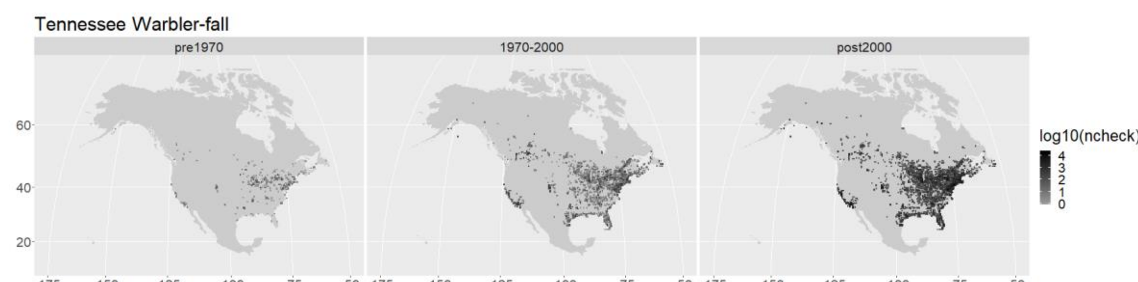
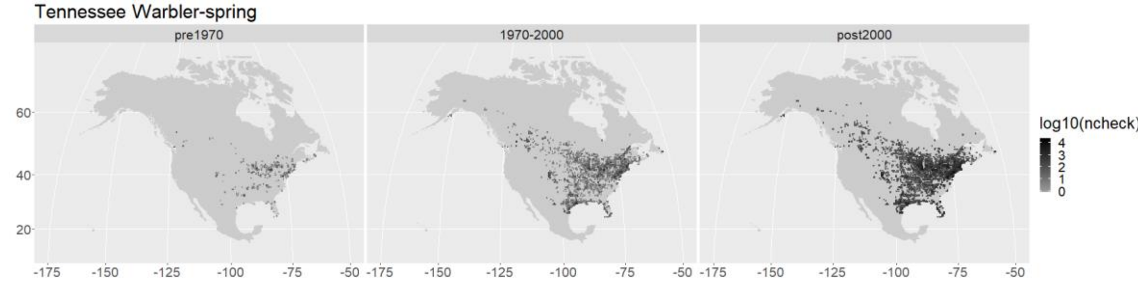
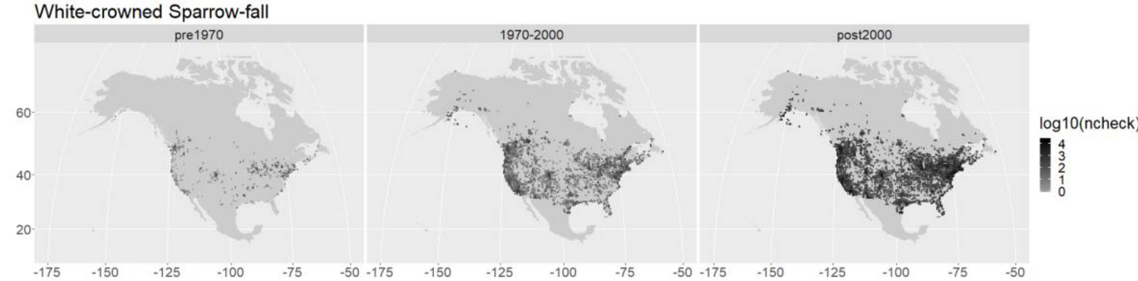

Tennessee Warbler-fall
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0

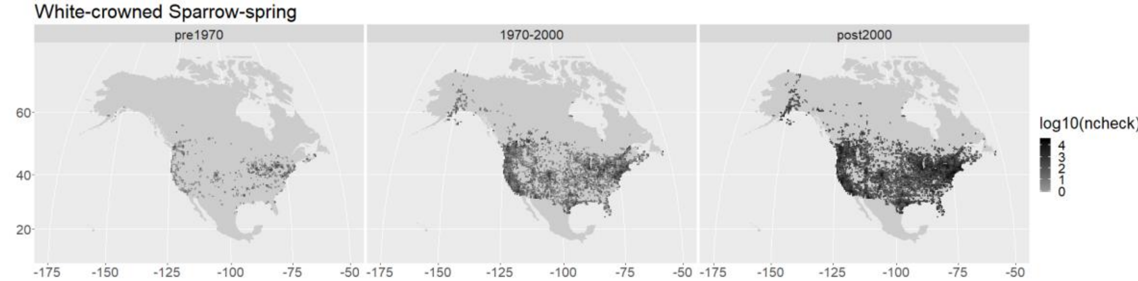
Tennessee Warbler-spring



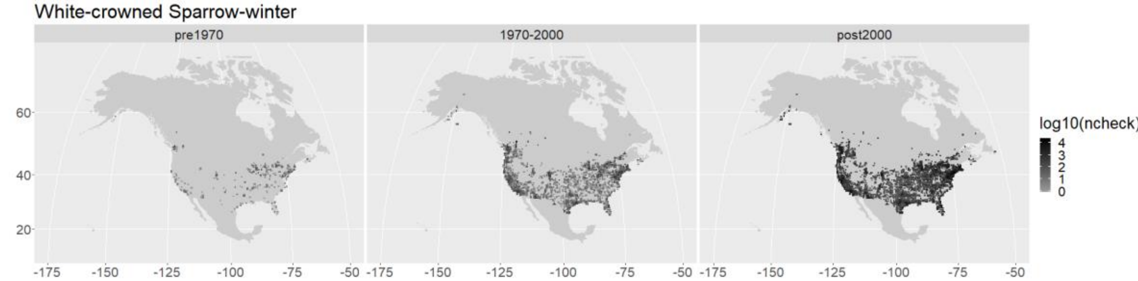
White-crowned Sparrow-fall



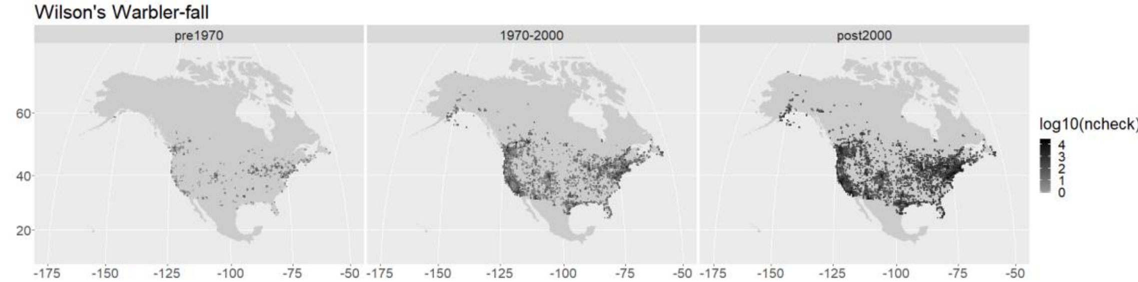
White-crowned Sparrow-spring

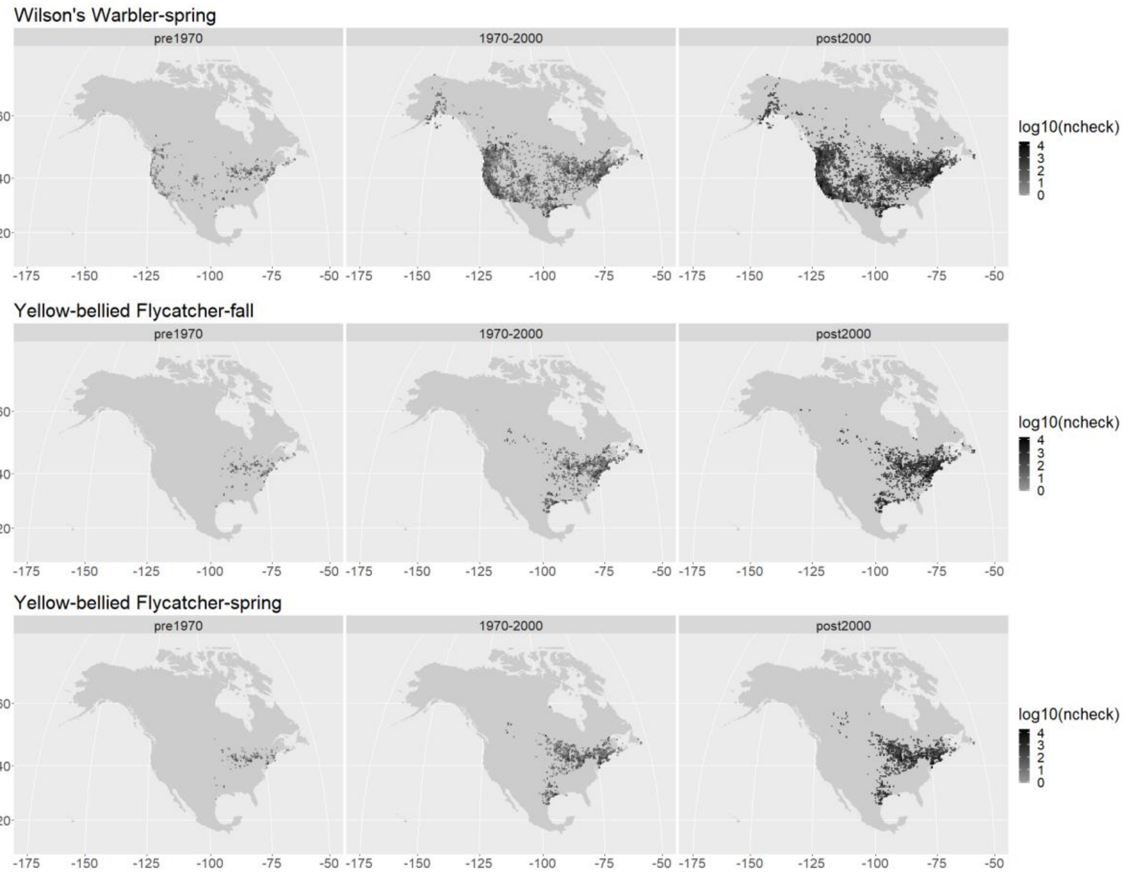


White-crowned Sparrow-winter



Wilson's Warbler-fall




Wilson's Warbler-spring
pre1970
1970-2000
post2000
log10(ncheck)
4
3
2
1
0
60
40
20
-175 -150 -125 -100 -75 -50
Yellow-bellied Flycatcher-fall
pre1970
1970-2000
post2000
log10(ncheck)
Yellow-bellied Flycatcher-spring
pre1970
1970-2000
post2000
log10(ncheck)

Appendix 3. Table of model estimates for the 40 by 40 km grid used as a random effect in the models, where the estimate is of the standard deviation for the grouping factor, rhat is the scale reduction factor, and ngrid is the number of grid cells included.

Species	Season	Estimate	Est.Error	Rhat	ngrid
American Tree Sparrow	fall	1.830	0.034	1.014	1596
	spring	1.717	0.033	1.112	1863
	winter	2.084	0.041	1.012	1839
Bald Eagle	fall	1.317	0.018	1.004	3583
	spring	1.303	0.016	1.018	4052
	winter	1.429	0.021	1.008	3215
Bay-breasted Warbler	fall	1.455	0.035	1.021	1263
	spring	0.949	0.022	1.000	1375
Blackpoll Warbler	fall	1.448	0.035	1.023	1319
	spring	1.166	0.022	1.016	2024
Black-throated Blue Warbler	fall	1.327	0.029	1.011	1271
	spring	1.559	0.033	1.003	1341
Blue-winged Warbler	fall	1.136	0.032	1.001	990
	spring	1.454	0.031	1.009	1386
Canada Warbler	fall	1.025	0.026	1.003	1276
	spring	1.127	0.025	1.008	1426
Cape May Warbler	fall	1.123	0.027	1.005	1180
	spring	1.101	0.025	1.006	1456
Connecticut Warbler	fall	0.850	0.051	1.000	330
	spring	0.876	0.048	1.001	365
Common Redpoll	fall	1.452	0.039	1.016	930
	spring	1.710	0.037	1.001	1250
	winter	1.757	0.033	1.000	1483
Evening Grosbeak	fall	1.616	0.034	1.013	1397
	spring	1.635	0.033	1.004	1546
	winter	1.908	0.044	1.004	1058
Gray-cheeked Thrush	fall	1.011	0.031	1.004	893
	spring	1.045	0.026	1.009	1227
Golden-winged Warbler	fall	1.161	0.045	1.000	542
	spring	1.400	0.036	1.004	1015
Harris's Sparrow	fall	2.197	0.071	1.017	658
	spring	1.753	0.054	1.019	825
	winter	2.074	0.055	1.012	824
Lapland Longspur	fall	1.460	0.037	1.010	1056
	spring	1.474	0.044	1.004	738
	winter	1.336	0.031	1.001	1168
Le Conte's Sparrow	fall	1.770	0.078	1.008	464
	spring	1.304	0.059	0.999	396

Species	Season	Estimate	Est.Error	Rhat	ngrid
Le Conte's Sparrow	winter	1.228	0.055	1.000	346
Least Flycatcher	fall	1.107	0.024	1.013	1834
	spring	1.241	0.021	1.055	2380
Magnolia Warbler	fall	1.565	0.028	1.003	1959
	spring	1.213	0.021	1.016	2050
Northern Parula	fall	1.359	0.024	1.009	1882
	spring	1.734	0.026	1.012	2661
Olive-sided Flycatcher	fall	1.099	0.022	1.001	1891
	spring	1.332	0.024	1.005	2258
Peregrine Falcon	fall	1.034	0.017	1.024	2516
	spring	1.093	0.018	1.003	2521
	winter	1.081	0.023	1.001	1346
Pine Siskin	fall	1.314	0.018	1.038	3243
	spring	1.452	0.020	1.050	3905
	winter	1.298	0.020	1.009	2896
Rusty Blackbird	fall	1.243	0.030	1.022	1496
	spring	1.327	0.026	1.009	1791
	winter	1.254	0.029	1.003	1324
Smith's Longspur	fall	1.570	0.272	1.001	31
	spring	2.099	0.225	1.004	65
	winter	1.701	0.215	1.001	43
Tennessee Warbler	fall	1.496	0.026	1.018	2018
	spring	1.400	0.025	1.005	2099
White-crowned Sparrow	fall	1.618	0.021	1.015	3458
	spring	1.493	0.017	1.038	4137
	winter	1.963	0.028	1.110	2506
Wilson's Warbler	fall	1.398	0.020	1.009	2810
	spring	1.570	0.025	1.012	2973
Yellow-bellied Flycatcher	fall	0.928	0.028	1.002	1058
	spring	1.071	0.031	1.003	894

Appendix 4. Table of the number of eBird checklists per decade within the seasonal ranges of the 28 species analyzed.

Species	Season	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Total
American Tree Sparrow	fall	97	187	272	674	2169	5379	9636	21250	139644	556695	736003
	spring	349	558	509	1566	3615	9564	15368	33095	206099	993860	1264583
	winter	166	475	460	1722	3512	8975	15023	32001	240557	1107423	1410314
Bald Eagle	fall		760	849	2947	5389	17436	35008	80091	508673	2143770	2794923
	spring	600	1425	1497	4725	8653	26612	48543	111664	698317	3095482	3997518
	winter	99	449	229	2108	3796	12225	23231	51383	374220	1802244	2269984
Bay-breasted Warbler	fall	184	318	308	1276	2183	5207	11128	21554	137184	592265	771607
	spring	212	353	422	1393	2183	6709	11818	24235	138957	601286	787568
Black-throated Blue Warbler	fall	211	401	394	1429	2795	6938	14382	28292	199878	871058	1125778
	spring	233	394	453	1645	2714	8501	14543	30291	220567	937894	1217235
Blackpoll Warbler	fall	234	359	402	1465	2814	6842	14470	28949	180379	780754	1016668
	spring	252	475	564	1627	2647	8343	14945	31743	186001	809115	1055712
Blue-winged Warbler	fall	43	322	108	495	1796	4360	9030	19658	132237	550810	718859
	spring	385	700	767	2436	3873	11820	19101	39699	270699	1060550	1410030
Canada Warbler	fall	149	351	288	1298	1793	5004	10958	22599	141880	584224	768544
	spring	252	511	551	1850	2825	8255	14303	31222	201806	797205	1058780
Cape May Warbler	fall	103	376	391	1150	2370	5957	12906	25149	160289	690954	899645
	spring	236	361	467	1462	2543	7386	13491	27451	161779	734302	949478

Species	Season	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Total
Common Redpoll	fall		59	79	75	744	4179	8769	16672	78465	343468	452510
	spring	246	370	222	994	2310	6831	11873	24285	138052	679423	864606
	winter	66	405	414	1488	3248	8422	14578	30283	211928	957311	1228143
Connecticut Warbler	fall	79	135	91	366	690	2288	5178	9974	68100	245970	332871
	spring	39	57	128	548	1153	2846	4305	7490	42478	162986	222030
Evening Grosbeak	fall			163	952	2994	9665	20279	41691	229508	949206	1254458
	spring			342	1637	3774	11147	21053	48733	240028	1084021	1410735
	winter	55		208	1253	2527	7570	14339	26054	145449	664977	862432
Golden-winged Warbler	fall		97	53	175	741	1377	3077	6048	51365	196491	259424
	spring	274	507	647	1318	2218	6340	11258	22897	144279	573987	763725
Gray-cheeked Thrush	fall	196	283	313	999	1766	3800	7564	15369	98906	418790	547986
	spring	238	422	441	1245	2019	6374	10802	22349	123268	534978	702136
Harris's Sparrow	fall		51	161	60	1009	3162	5024	9191	54044	191983	264685
	spring			63	229	423	1758	4391	13331	69396	289512	379103
	winter				200	706	2647	5084	17508	93520	419553	539218
Lapland Longspur	fall		244	168	335	2084	6328	11710	26032	126566	531513	704980
	spring		137	203	708	1833	6198	9894	16314	84672	431211	551170
	winter		244	224	746	1957	5560	8918	19071	137776	680669	855165
Le Conte's Sparrow	fall	23	126	99	413	310	1414	4138	9522	47314	159066	222425
	spring		104	128	362	265	1932	4718	11466	54990	201755	275720
	winter				356	78	815	2146	7145	37579	152248	200367

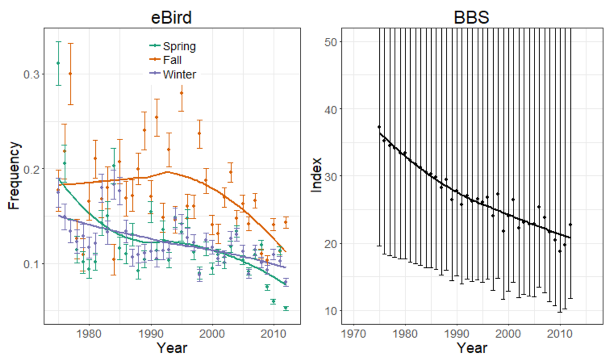
Species	Season	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Total
Least Flycatcher	fall	180	400	371	1509	2571	7538	15513	37067	225202	920303	1210654
	spring	279	550	738	2194	3726	11767	21056	46761	280031	1117477	1484579
Magnolia Warbler	fall	200	410	366	1699	2695	8404	16058	33598	212335	921344	1197109
	spring	284	566	718	2033	3140	9407	17287	37159	245626	1016651	1332871
Northern Parula	fall	233	525	492	1993	3171	9061	19096	42316	263709	1143675	1484271
	spring	465	873	1041	3158	4573	15854	27717	66246	424578	1726455	2270960
Olive-sided Flycatcher	fall	71	282	150	1130	2587	6624	13994	32782	184418	742875	984913
	spring	168	294	419	1142	2852	10542	19958	49115	248828	1012694	1346012
Peregrine Falcon	fall	160	728	840	2585	5661	15435	31501	75980	461089	1932069	2526048
	spring	572	1063	1399	2850	5818	23271	41348	99606	577402	2522428	3275757
	winter	66	141	91	492	2684	9818	17617	41178	282558	1390589	1745234
Pine Siskin	fall	259	389	613	1564	4842	14762	29971	68905	409956	1724260	2255521
	spring	549	1008	1333	4163	7807	24000	44775	102287	607476	2797155	3590553
	winter	98	466	459	2000	3741	11738	22840	50136	367451	1760789	2219718
Rusty Blackbird	fall	168	387	410	1424	2962	8625	15409	30651	198767	821470	1080273
	spring	609	977	832	3060	4762	13570	21270	42431	282544	1365724	1735779
	winter	165	371	306	1887	2625	7368	11133	26138	193086	907090	1150169
Smith's Longspur	fall								23	623	2992	3638
	spring			43	48	511	178	58	558	5983	24717	32096
	winter				84			410	950	1917	10058	13419
Tennessee Warbler	fall	245	478	550	2093	3408	9333	18789	40764	253948	1083816	1413424
	spring	268	463	579	1726	2814	8615	15744	33298	180089	789506	1033102

Species	Season	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Total
White-crowned Sparrow	fall	164	377	554	1550	4308	11807	23906	58688	354512	1480915	1936781
	spring	691	1111	1169	3553	6797	21001	37944	92150	523906	2455939	3144261
	winter	171	367	112	1945	3566	10649	19868	47172	330909	1592211	2006970
Wilson's Warbler	fall	231	383	439	1863	3839	10984	24182	56082	314548	1321875	1734426
	spring	207	418	517	1622	3416	12467	23925	58827	291857	1287595	1680851
Yellow-bellied Flycatcher	fall	131	315	285	504	1512	4449	9938	21212	125592	508638	672576
	spring	64	129	183	621	1192	5172	8730	19956	105101	401745	542893

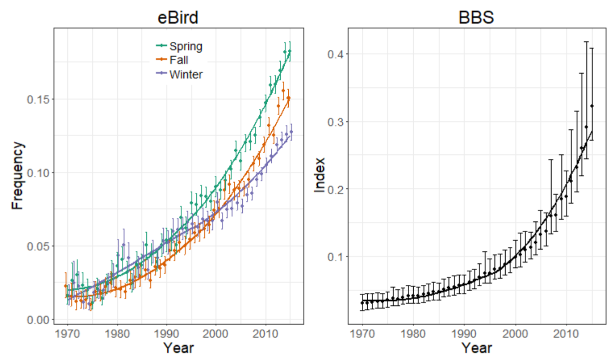
Appendix 5. Annual indices and 95% credible intervals by season for the 28 species analyzed, including loess smooths with spans of 0.2.

Appendix 6. Plots of eBird annual indices with their 95% credible intervals and smoothed trajectories (LOESS with a span of 1) adjacent to those from models of BBS data, for each of the species for which data were available from BBS. The y-axis was truncated on BBS plots for several species with large credible intervals, so that the estimated trajectory was evident.

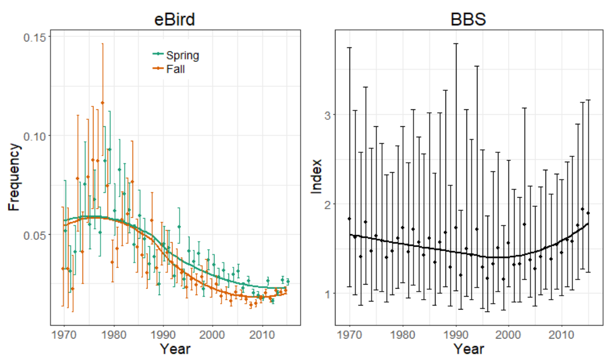
American Tree Sparrow



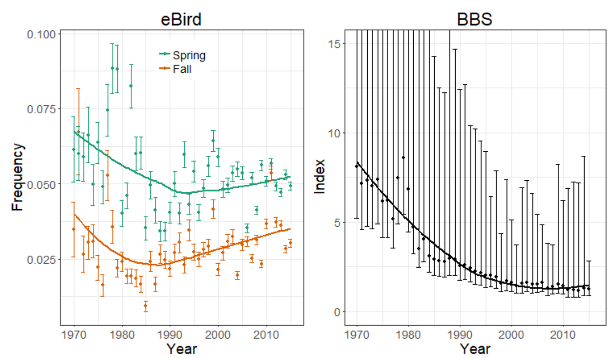
Bald Eagle



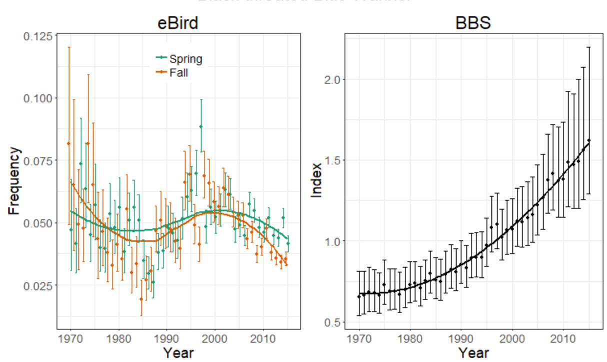
Bay-breasted Warbler



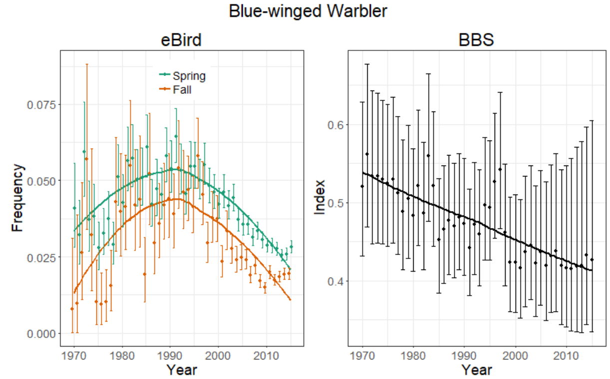
Blackpoll Warbler

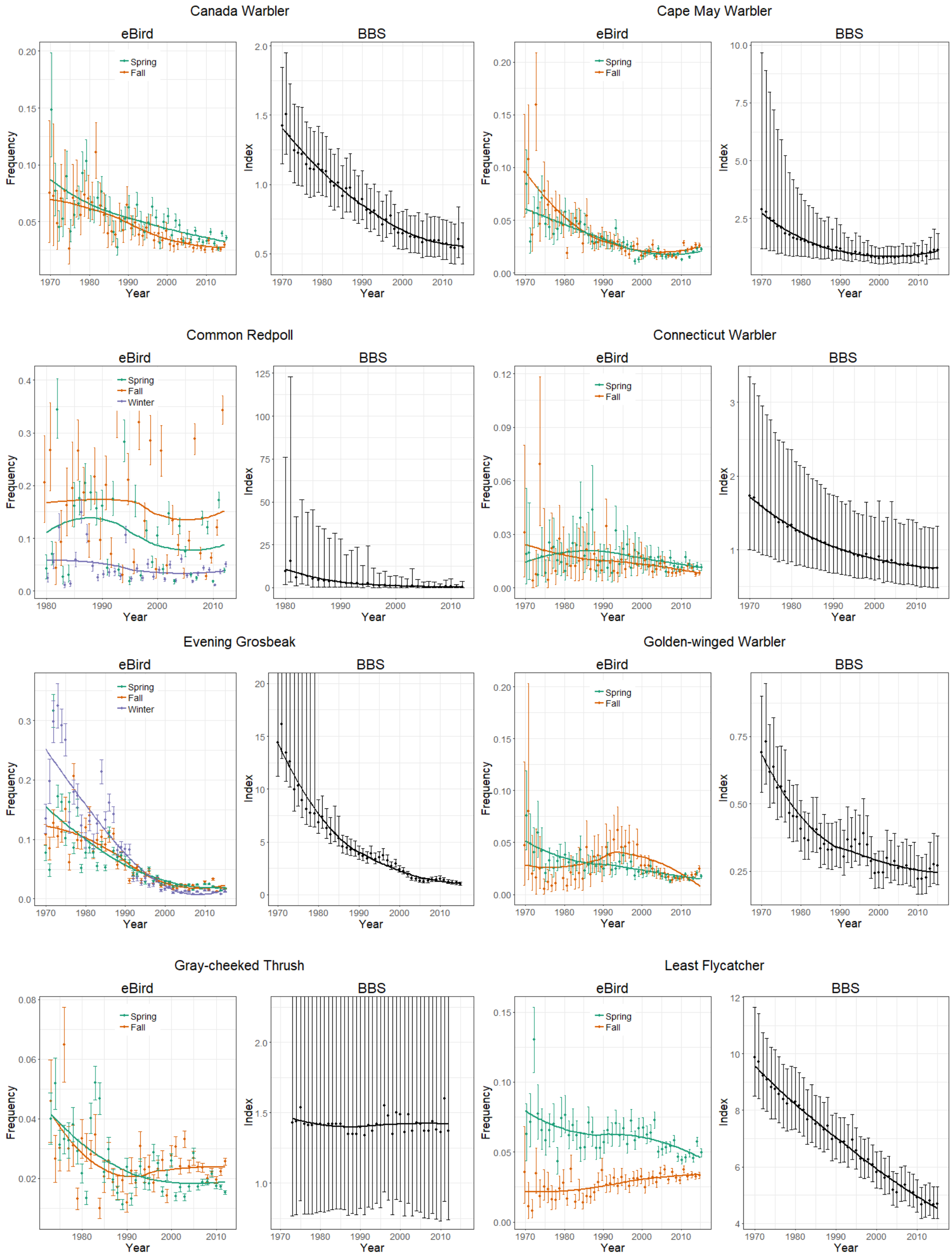


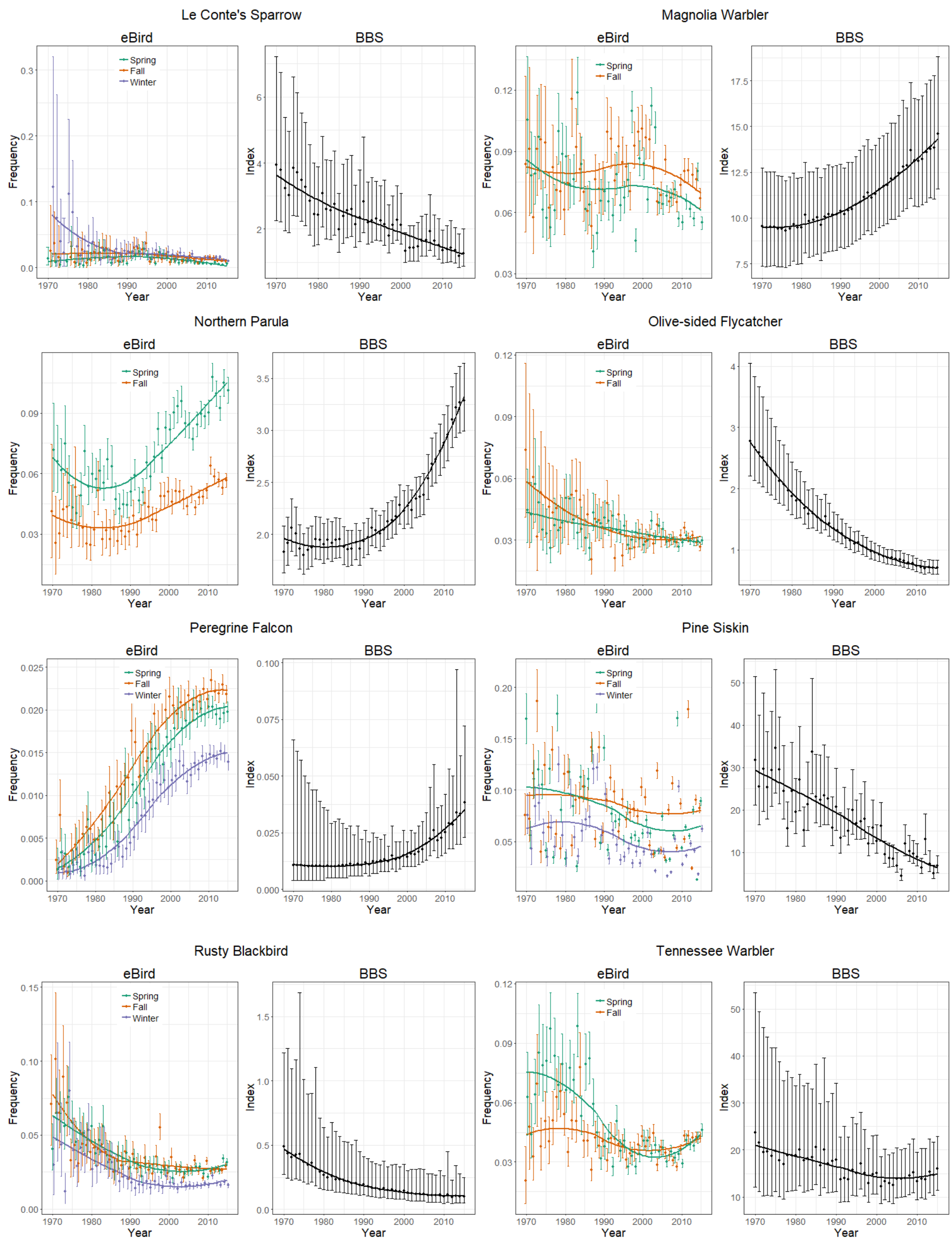
Black-throated Blue Warbler

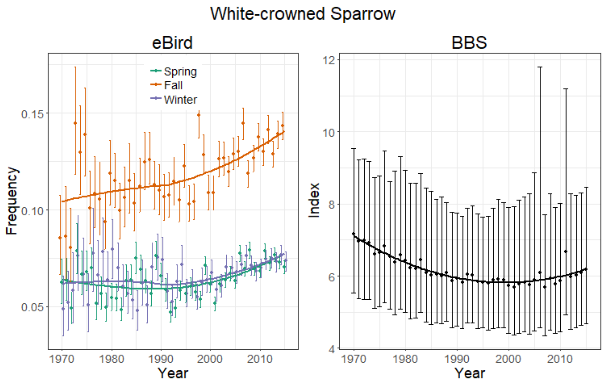


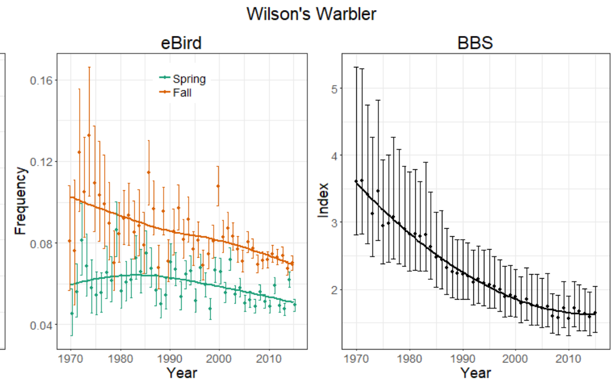
Blue-winged Warbler

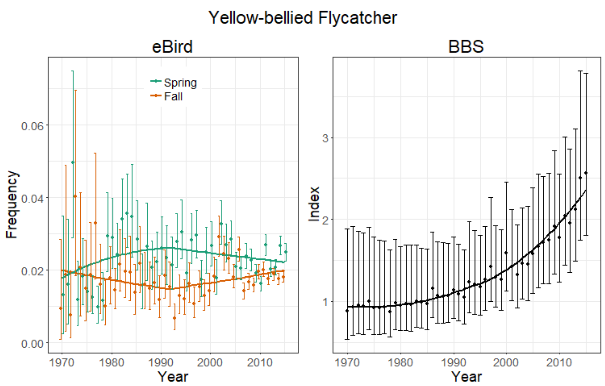



Canada Warbler
eBird
BBS
Cape May Warbler
eBird
BBS
Common Redpoll
eBird
BBS
Connecticut Warbler
eBird
BBS
Evening Grosbeak
eBird
BBS
Golden-winged Warbler
eBird
BBS
Gray-cheeked Thrush
eBird
BBS
Least Flycatcher
eBird
BBS
Spring
Fall
Winter
Frequency
Index
Year


Le Conte's Sparrow
eBird
Spring
Fall
Winter
Frequency
Year
BBS
Index
Year
Magnolia Warbler
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year
Northern Parula
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year
Olive-sided Flycatcher
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year
Peregrine Falcon
eBird
Spring
Fall
Winter
Frequency
Year
BBS
Index
Year
Pine Siskin
eBird
Spring
Fall
Winter
Frequency
Year
BBS
Index
Year
Rusty Blackbird
eBird
Spring
Fall
Winter
Frequency
Year
BBS
Index
Year
Tennessee Warbler
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year


White-crowned Sparrow
eBird
Spring
Fall
Winter
Frequency
Year
BBS
Index
Year


Wilson's Warbler
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year


Yellow-bellied Flycatcher
eBird
Spring
Fall
Frequency
Year
BBS
Index
Year