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# No evidence of overall changes in spatial population synchrony across bird species in North America

Master's thesis in Biology

Supervisor: Brage Bremset Hansen

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Faculty of Natural Sciences

Department of Biology



Kunnskap for en bedre verden





## Abstract

When populations show strongly correlated fluctuations in abundances through time, they have a high degree of spatial population synchrony. This is often associated with an increased risk of species extinction. Spatially autocorrelated environmental noise (such as weather fluctuations) affecting local populations is an important mechanism contributing to spatial population synchrony. Consequently, changes in the spatial autocorrelation of environmental noise due to, for instance climate change, can drive a change in spatial population synchrony. Here, I analysed data from 1975 to 2019 for 33 North American bird species from the North American Breeding Bird Survey and Waterfowl Breeding Population and Habitat Survey to investigate whether there has been a trend in spatial population synchrony across species. Similarly, I tested for changes in the spatial autocorrelation of mean annual temperature and total annual precipitation in the same regions and time period. I used the moving windows approach with the mean of a pairwise correlation matrix to estimate the spatial synchrony per 3-year window. I fitted a linear mixed effect model to test for the change in spatial population synchrony across species and linear models to test the change in spatial autocorrelation of temperature and precipitation. The trends in average spatial population synchrony across species at short (0 – 500 km), intermediate (500 – 1000 km) and long distances (> 1000 km) were not statistically significant. The estimated trends of spatial autocorrelation in temperature and precipitation were also not statistically significant. At the individual species level, six species showed a significant change in spatial population synchrony, but this was expected due to chance with a significance level of 0.05. Thus, I found no evidence of an overall trend in spatial population synchrony over time for the species analysed. However, there were noise and sources of error in the data analysed which could have influenced my results. Considering the importance of investigating spatial population synchrony regarding extinction risk and conservation, there is a need for more multispecies studies on this research topic.

## Sammendrag

Populasjoner med sterkt korrelerte årlige fluktuasjoner i populasjonsstørrelse, har høy romlig populasjonssynkronitet. Dette øker ofte risikoen for utryddelse hos en art. Romlig autokorrelasjon i miljøstøy (eks. fluktuasjoner i værvariabler) er en mekanisme som kan påvirke romlig populasjonssynkronitet. Klimaendringer kan føre til endringer i romlig autokorrelasjon i miljøstøy. Dette kan videre påvirke den romlige populasjonssynkroniteten. Jeg analyserte data for 33 nord-amerikanske fuglearter fra North American Breeding Bird Survey og Waterfowl Breeding Population and Habitat Survey i tidsperioden fra 1975 til 2019. Jeg undersøkte om det er en trend i romlig populasjonssynkronitet på tvers av artene, og for endringer i romlig autokorrelasjon i årlig gjennomsnittstemperatur og total årlig nedbør i samme tidsperiode og region. Jeg estimerte romlig populasjonssynkronitet med fremgangsmåten moving window, hvor gjennomsnittet av en parvis korrelasjonsmatrise ble kalkulert per vindu (3 år). For å estimere endringen i romlig populasjonssynkronitet på tvers av artene brukte jeg en lineær miksemodell. Jeg brukte lineære modeller for å undersøke endringer i romlig autokorrelasjon av temperatur og nedbør. De estimerte trendene for gjennomsnittlig romlig populasjonssynkronitet på korte (0 – 500 km), mellomlange (500 – 1000 km) og lange avstander (> 1000 km) på tvers av arter var ikke statistisk signifikante. Trenden for romlig autokorrelasjon i temperatur og nedbør var heller ikke statistisk signifikante. På individnivå hadde seks arter statistisk signifikant trend i romlig populasjonssynkronitet, men dette var forventet med signifikansnivået 0.05. Jeg fant ingen bevis for en generell trend i romlig populasjonssynkronitet over tid for de artene som ble analysert. Resultatene kan derimot blitt påvirket av støy og feilkilder i dataen. Siden forskning på romlig populasjonssynkronitet kan gi informasjon om utryddelse og dette kan være verdifullt for bevaring av naturmangfold, vil studier på tvers av arter på dette temaet være nyttig.

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## Introduction

Population sizes naturally fluctuate through time due to birth, death, emigration, and immigration of individuals (Gotelli, 2008). Separated populations can have similar population dynamics due to, for instance, the environment influencing the populations in the same way (Elton, 1924). Spatial population synchrony is the correlation of fluctuation in abundances among intraspecific populations through time, typically declining with increasing distance among populations (Elton, 1924; Moran, 1953; Ranta et al., 1995). Spatial population synchrony is mainly caused by three mechanisms: spatial autocorrelation (i.e. correlation with itself) of the environment, dispersal, and trophic interactions (Moran, 1953; Ranta et al., 1995; Koenig, 1999; Ims & Andreassen, 2000). When two or more populations have identical forms of linear density dependence and have no dispersal among them, the correlation among populations in log abundance is expected to be equal to the spatial autocorrelation of the environmental noise (e.g. weather fluctuations) acting on the populations (Moran, 1953; Royama, 1992). This is called the Moran effect. Furthermore, intraspecific populations that are near each other often experience a similar change in the environment (e.g. temperature) and thus high spatial autocorrelation in environmental noise. High spatial population synchrony is associated with an increased risk of global extinction (Heino et al., 1997; Engen et al., 2002). If intraspecific populations are highly synchronized and have low population sizes, they might all crash simultaneously and thus become extinct. In contrast, if the populations have low spatial population synchrony, even if some populations crash others will persist, decreasing the probability of extinction.

Recent theoretical (Ranta et al., 1997a; Lande et al., 1999; Kendall et al., 2000; Engen & Sæther, 2005; Allstadt et al., 2015; Hansen et al., 2020) and empirical work (Post & Forchhammer, 2002; 2004; Sæther et al., 2007; Hansen et al., 2013; Allstadt et al., 2015; Koenig & Liebhold, 2016; Sheppard et al., 2016; Kahilainen et al., 2018; Dallas et al., 2020) suggests that large-scale environmental change may impact spatial population synchrony. Climate change has already influenced a range of environmental variables across the globe and predictions indicate that these changes will only become more severe in the future (IPCC, 2021). There is currently a global change in the mean environment, with some regions becoming wetter while others drier and the global temperature is steadily increasing. At the same time, extreme weather events (e.g. heavy precipitation, drought and heatwaves) are increasing in frequency (IPCC, 2021). Changes in the mean environment can directly influence spatial population synchrony

by affecting the vital rates (i.e. survival, reproduction and growth rate; Barbraud & Weimerskirch, 2001; Molnár et al., 2010) and carrying capacity of populations (Sæther et al., 2000; Engen & Sæther, 2005). Changes in the vital rates and carrying capacity can affect the annual fluctuations in population size and if several populations are affected similarly, spatial population synchrony might increase. Furthermore, extreme weather events can force populations to be synchronized due to impacts over large areas and thus affect several populations and species simultaneously (Hansen et al., 2013; Hansen et al., 2020). In contrast, if these extreme events occur locally, they might have a desynchronising effect (Hansen et al., 2019a). There is spatial variation in the environment and there are differences in the responses among populations to the environment, as illustrated by environmental variables affecting population dynamics of geographically separated populations differently (Engen & Sæther, 2005; Anders & Post, 2006; Grøtan et al., 2008; Sæther et al., 2008; Hansen et al., 2019b). This heterogeneity in response can result in the spatial population synchrony being lower than the autocorrelation of the environment (Herfindal et al., 2022). Furthermore, a changing environment could affect the spatial variation in the environment and thus potentially change the heterogeneity in populations' response to the environment (Engen & Sæther, 2005; Hansen et al., 2020). Additionally, in populations that have large demographic stochasticity and low population size, demographic stochasticity can have a desynchronising effect on the fluctuations (Sæther et al., 2007). Furthermore, Sæther et al. (2007) observed that demographic stochasticity can reduce the effect of the spatial autocorrelation of environmental noise on spatial population synchrony. Thus, there is potential for change in spatial population synchrony along several pathways because of climate change.

Among the various mechanisms influencing spatial population synchrony, a change in the spatial autocorrelation of environmental noise can have a significant effect on the changes in spatial population synchrony (Ranta et al., 1997a; Koenig, 2002; Post & Forchhammer, 2004; Allstadt et al., 2015; Sheppard et al., 2016). Further, Di Cecco and Gouhier (2018) observed that climate change has impacted the spatial and temporal autocorrelation of temperature at a global and regional scale. Moreover, they predicted that the temporal and spatial autocorrelation will continue to increase with future climate change, which consequently can cause changes in spatial population synchrony. Indirectly, climate change can also influence spatial population synchrony through the effect on dispersal rate, habitat fragmentation and trophic interactions (Ims & Andreassen, 2000; Bellamy et al., 2003; Hansen et al., 2020). Furthermore, the different

mechanisms of climate-induced change in spatial population synchrony make it difficult to disentangle the effects from each other, especially the environment and dispersal since the environment can influence dispersal (Ranta et al., 1995; Kendall et al., 2000). Climate change can directly affect the dispersal rate by, for instance, increasing the spring temperature (Pärn et al., 2012) and influencing flooding (Roche et al., 2012). Indirectly, climate change can influence the dispersal rate by reducing habitat quality (Figuerola, 2007) and body size which plays an important role in the ability to disperse (McCauley & Mabry, 2011). Dispersal can increase spatial population synchrony by allowing an “excess” of individuals from populations with higher growth rates to move to populations with lower growth rates. Thus, reducing the variation in growth rates among populations resulting in more similar fluctuations. However, the effect of dispersal on spatial population synchrony is stronger over shorter distances than longer distances (Ranta et al., 1995; Ranta et al., 1997b; Lande et al., 1999). Interactions between species at different trophic levels may also induce spatial population synchrony. Nomadic predators can have a synchronizing effect on the prey populations by travelling between prey hotspots (Ydenberg, 1987; Ims & Andreassen, 2000; Jarillo et al., 2020). There are, however, other factors that can also influence the degree of spatial population synchrony, such as life-history strategies (Tedesco & Hugueny, 2006; Marquez et al., 2019) and harvesting (Jarillo et al., 2020). Thus, there are several pathways through which climate change can induce changes in spatial population synchrony both directly and indirectly (Hansen et al., 2020).

Research into changes in spatial population synchrony has mainly been studies of single species (Post & Forchhammer, 2004; Allstadt et al., 2015; Tack et al., 2015; Kahilainen et al., 2018). These studies give valuable insight for understanding and disentangling the mechanisms causing a change in spatial synchrony and can indicate which “type” of species are more likely to experience a change in spatial population synchrony. The estimates of changes in spatial population synchrony at the single-species level are difficult to generalize to other species and thus researching multiple species might increase the power to detect a common trend, especially when studying multiple species belonging to the same taxonomic class and hence more likely to show similar responses to environmental fluctuations. A handful of studies have found that spatial population synchrony among Glanville Fritillary Butterfly (*Melitaea cinxia*), Caribou (*Rangifer tarandus*) and some moth, aphid, and bird species has increased over time and that changes in the spatial autocorrelation of temperature or precipitation were the likely cause of these changes (Post & Forchhammer, 2004; Allstadt et al., 2015; Tack et al., 2015; Koenig &

Liebhold, 2016; Sheppard et al., 2016; Kahilainen et al., 2018; Dallas et al., 2020). Koenig and Liebhold (2016) investigated changes in spatial population synchrony among 49 North American bird species by using pairwise correlation matrixes, the moving window approach and a linear model. They observed a general increase in spatial population synchrony at sites 0 – 250 km apart (69% of the species), 250 – 500 km (63% of the species) and sites 500 – 1000 km apart (65% of the species). They identified the likely driver of this change as the increase in the autocorrelation of mean maximum temperature. Even though a large proportion of 49 bird species experienced a significant change in spatial population synchrony, there was still a large number of species that did not experience any significant changes and the changes in spatial population synchrony differed between the distance intervals within species. There is possibly a large heterogeneity between species and thus there is a need for more multispecies studies to better understand if the trends observed are general or only species-specific.

Here I analysed temporal changes in spatial population synchrony in 33 bird species breeding in North America. In addition, I tested for changes in spatial autocorrelation of temperature and precipitation to investigate whether any trends in spatial autocorrelation of the environment were reflected in trends in the spatial synchrony of populations. By doing this, I aimed to extend our knowledge about whether changes in spatial population synchrony are mostly species-specific or can be generalised across groups of species. To investigate the change in spatial population synchrony, I used population count data from 1975 to 2019 from two datasets: the North American Breeding Bird Survey (BBS) and Waterfowl Breeding Population and Habitat Survey (WBPHS). The BBS has surveyed breeding bird species in the U.S and Canada for over 50 years. The WBPHS has studied waterfowl species in Canada and Alaska, as well as some parts of the north-central U.S for over 60 years. These publicly available datasets are large geographic scale surveys on population counts on bird species and were chosen based on their long time series of multiple species and similar geographic coverage. Furthermore, these datasets are surveyed in the same geographical region as the data analysed by Koenig and Liebhold (2016) and they and I used similar methods for analysing changes in spatial population synchrony thus making the studies comparable.

## Methods

### *Waterfowl Breeding Population and Habitat Survey*

The Waterfowl Breeding Population and Habitat Survey (WBPHS) has been conducted annually by the U.S Fish and Wildlife Service and Canadian Wildlife Service in the northern United States and Canada since 1955 (Smith, 1995). The Traditional Survey Area includes Alaska, part of the north-central U.S, and the western part of Canada. The survey is conducted from May to June, but the exact survey period varies depending on the region and habitat type. Waterfowl are counted by a two-person crew surveying 400m wide transects from an airplane. Each transect is divided into segments that are approximately 29 km long and these segments are surveyed from 1 to 2 hours after sunrise to noon. The survey area is divided into 52 strata, determined by habitat type and political boundaries (Fig. 1) and each stratum contain several transects. Visibility correction factors determined by ground crews surveying a sample of the segments were available, but these were calculated differently for different regions and years (Smith, 1995). I have therefore used the raw unadjusted data counted by the aerial crew. The WBPHS data was received from the U.S Fish and Wildlife Service and included population count data for 20 species from 1955 to 2019.

### *North American Breeding Bird Survey*

The North American Breeding Bird Survey (BBS) is a large scale survey coordinated by the United States Geological Survey and the Canadian Wildlife Service that has been conducted annually since 1966 (Robbins et al., 1986; Sauer et al., 2017). The data is collected at the peak of the breeding season each year, which on average is June but ranges from late May in the southern states to early July in Canada. The observer selects the sampling date as close to previous years as possible to reduce sampling variability. The survey starts 30 min before local sunrise. The routes are along roadsides and are approximately 40 km long and every 800 m the observer stops, for a total of 50 stops. At each stop, the observer counts the total number of each species seen or heard within a 400 m radius during a 3-minute point count. I retrieved the BBS data from the R package *bbsBayes* (v2.3.8.2020; Edwards & Smith, 2021), which contained population count data for 738 species with observations spanning from 1966 to 2019.



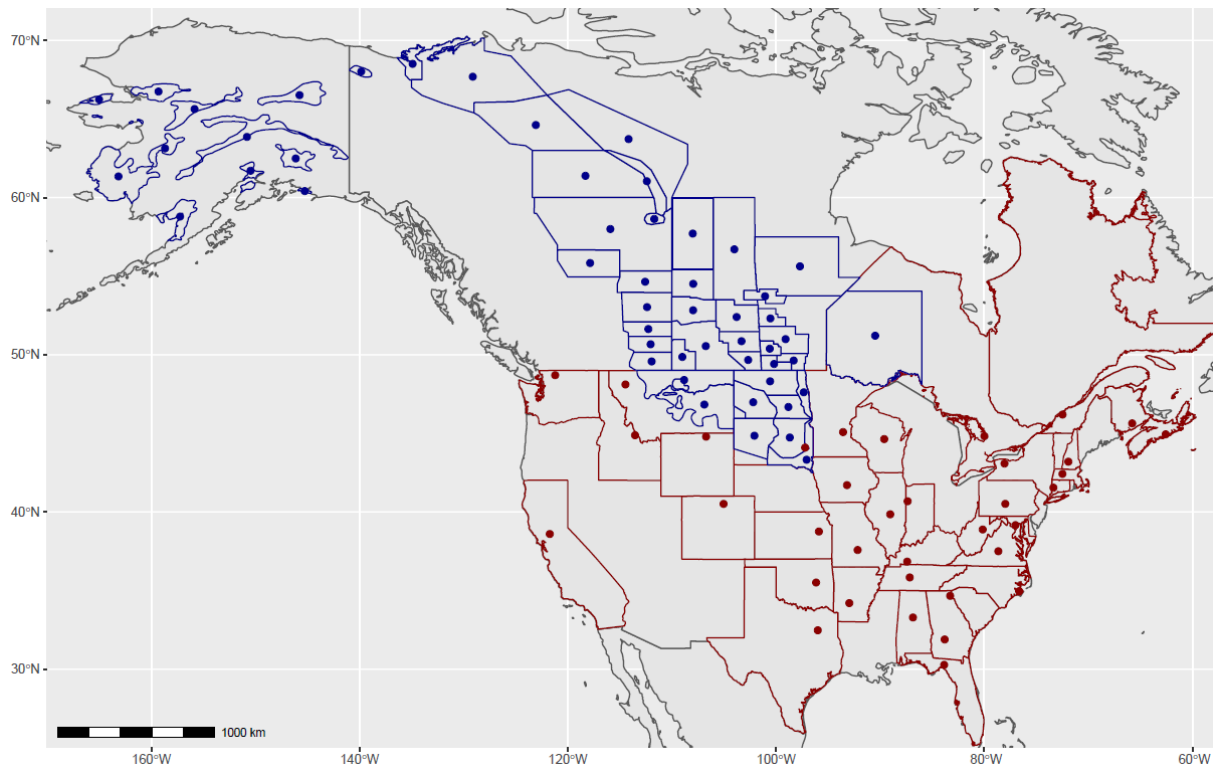


Figure 1: Map of distribution of population centroids based on the sampled routes and transects. The red dots are centre coordinates for BBS sites, aggregated by state and Canadian province ( $n = 36$  sites) and the blue dots are centre coordinates for WBPHS populations, aggregated by survey stratum ( $n = 67$  sites). The weather data was aggregated at the state and Canadian province level for BBS and stratum level for WBPHS. Only the sites that were used in the analysis are shown.

### *Data processing*

Data processing was an important step in the analysis and considerable time was used to establish criteria and filter out unwanted data. These steps were carried out identically on both datasets to ensure that they were as comparable as possible. The data processing steps were establishing a common time frame, removing transects and routes that were not surveyed each year, aggregating by strata, states and provinces, dividing into distance intervals and lastly removing the species that had fewer than 10 pairwise correlations between sites. The time frame from 1975 to 2019 was used in the analysis, as few routes that were established in the period between 1966 and 1974 were surveyed every year until 2019, resulting in few species containing at least 10 pairwise correlations with sites. I deemed it more important to increase

the number of species than to include additional years in the analysis since I was investigating changes in spatial population synchrony across species. The data were aggregated by stratum for the WBPBS and state and province for the BBS, and these were used as proxies for populations. The centre point of each stratum, state and province was determined by the mean coordinates of the transects/routes (Fig. 1). From the year the surveys were started (WBPBS in 1955 and BBS in 1966) until 2019, several new transects (WBPBS) and routes (BBS) have been established. Consequently, the increase in effort in the later decades could result in higher population counts and thus may influence the change in spatial population synchrony. Therefore, the counts were recalculated for each site (strata, states and provinces) based only on the transects and routes that have been surveyed every year within the time frame established. The pairwise estimates of spatial population synchrony were divided into three distance intervals to investigate the effect of distance on the change in spatial population synchrony. Short distances contained the pairwise sites where the distance was equal to or less than 500 km, intermediate distances contained pairs with distances between 500 – 1000 km and long distances contained the remaining pairwise sites more than 1000 km apart. The pairwise distance matrix between sites was calculated using the R package *geosphere* (v1.5-14; Hijmans et al., 2021). Species with fewer than 10 pairwise correlations between sites in each distance interval were excluded from the analysis. After the filtering of the data, 10 of 20 species from the WBPBS and 23 of 738 species from the BBS were used in the analysis (Table A1).

### *Weather data*

I analysed mean annual temperature and total annual precipitation in the strata, states and provinces for which I analysed spatial population synchrony. I obtained data from 1975 to 2019 from the National Oceanic and Atmospheric Administration (NOAA, 2022) and the Government of Canada (Government of Canada, 2022). The data were aggregated so the sites with environmental data matched the size and location of the strata, states and provinces from the WBPBS and BBS. Temperature and precipitation were chosen as the climatic variables due to the accessibility of data and their documented effect on bird population dynamics (Sæther et al., 2000; Jenouvrier, 2013; Cumming et al., 2014). Annual values were chosen as opposed to seasonal variables (e.g. winter temperature and spring precipitation) since the species would likely be affected differently among different seasonal variables and thus choosing the optimum seasonal variables that fit every species would be troublesome.

## *Data analysis*

Change in spatial population synchrony was estimated by measuring the correlation of log abundance of intraspecific populations divided into non-overlapping moving windows of 3 years. The estimated spatial population synchrony ranged from -1 to 1, where populations with spatial synchrony of 1 have a perfect positive correlation, at 0 the populations fluctuate independently, and at -1 they have a perfect negative correlation. Based on simulations from Le Moullec et al. (2021), assuming no observation error, a window length of 3 years with no overlap had the highest ability to detect a true change in spatial population synchrony. These simulations analysed a synthetic dataset with 20 populations spanning 50 years. Increasing the window length would decrease the ability of the moving windows to detect a true change and decrease the precision. Overlapping the windows would use the same data twice and thus introduce bias due to pseudoreplication. A pairwise correlation matrix across all populations of a species was calculated within the window and the chosen distance interval. The mean of the lower triangular pairwise correlation matrix was the estimated spatial population synchrony for that species in that window and distance interval. This was repeated for a total of 15 windows spanning 45 years for 33 species. Due to the way the pairwise correlation matrix was calculated, if all the counts were the same for one population within the window the standard deviation was zero and the pairwise correlation with that population was not possible to calculate. This was likely caused by very small population counts, as in many cases only a few individuals were counted for a population. This occurred in 23 windows among 15 species in the BBS and 13 windows among 4 species in the WBPHS. To work around this problem, a small amount of random noise was added (using the jitter function in R) to the population counts ensuring that the counts can't be identical.

To test whether spatial population synchrony has changed over time I fitted a linear mixed effect model with the R package lme4 (v1.1-28; Bates et al., 2015). The response variable was the estimated spatial population synchrony per window for each species. The fixed effects were distance intervals with two-way interaction with both time (window) and dataset. In this model I was interested in the change in spatial population synchrony across species and species was therefore included as a random effect on the intercept to account for the variability in intercept between species. Time was included as a random effect on the slope to allow the relationship between time and spatial population synchrony to vary among species (Zuur et al., 2009). In addition to the linear mixed effect model across all species, I fitted a linear model for each

species with spatial population synchrony as response variable and time as predictor variables repeated for the distance intervals.

The regional synchrony (i.e. the degree of synchrony across distance) was estimated using the `sncf` function from the R package `ncf` (v1.3-2; Bjørnstad, 2022) with 1000 resampling using bootstrapping. The confidence intervals were based on the 2.5% and 97.5% quantiles. This was repeated for each species to get the species-specific estimates.

To quantify the change in spatial autocorrelation of mean annual temperature and total annual precipitation, I used the same moving windows analysis as for the BBS and WBPHS data, with identical overlap, length of windows, and distance intervals. I fitted a linear model with the estimated spatial autocorrelation as the response variable and time as the predictor variable. I used R version 4.1.2 for all my statistical analyses (R Core Team, 2021).

## Results

The trend in spatial population synchrony across all species (across WBPHS and BBS) at short (0 – 500 km), intermediate (500 – 1000 km) and long distances (> 1000 km) were not significantly different from each other. There was no evidence of an effect of time (3-year window) on spatial population synchrony at short ( $\beta = -0.002$ ,  $SE = \pm 0.001$ ,  $t = -1.19$ ,  $p = 0.24$ ), intermediate ( $\beta = -0.002$ ) and long distances ( $\beta = 0.006$ , Table 1 & Fig. 2). The conditional  $R^2$  (Table 1) indicate that the fixed effects (window, distance interval and window) and random effects (species and window) didn't explain much of the variation in the estimated spatial population synchrony. These results indicate a common lack of temporal trend in spatial population synchrony across the distance intervals.

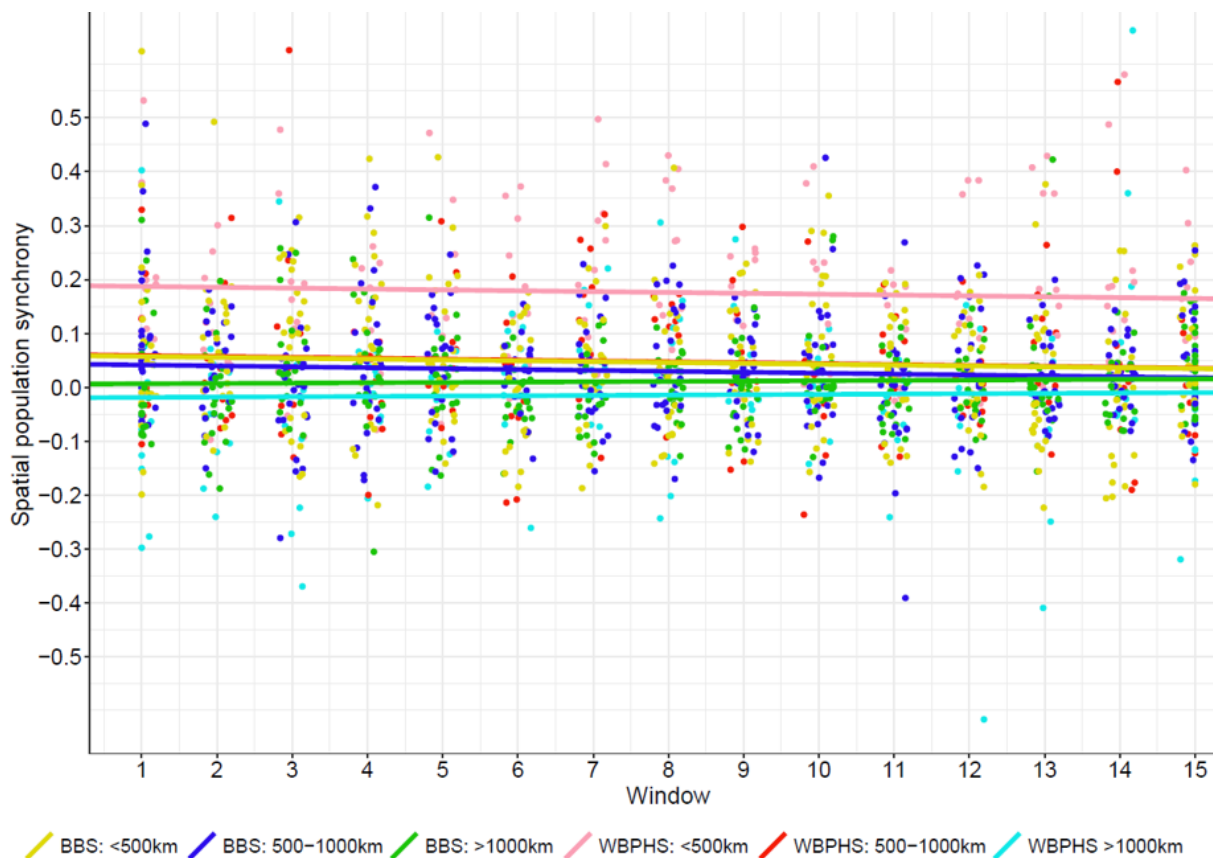


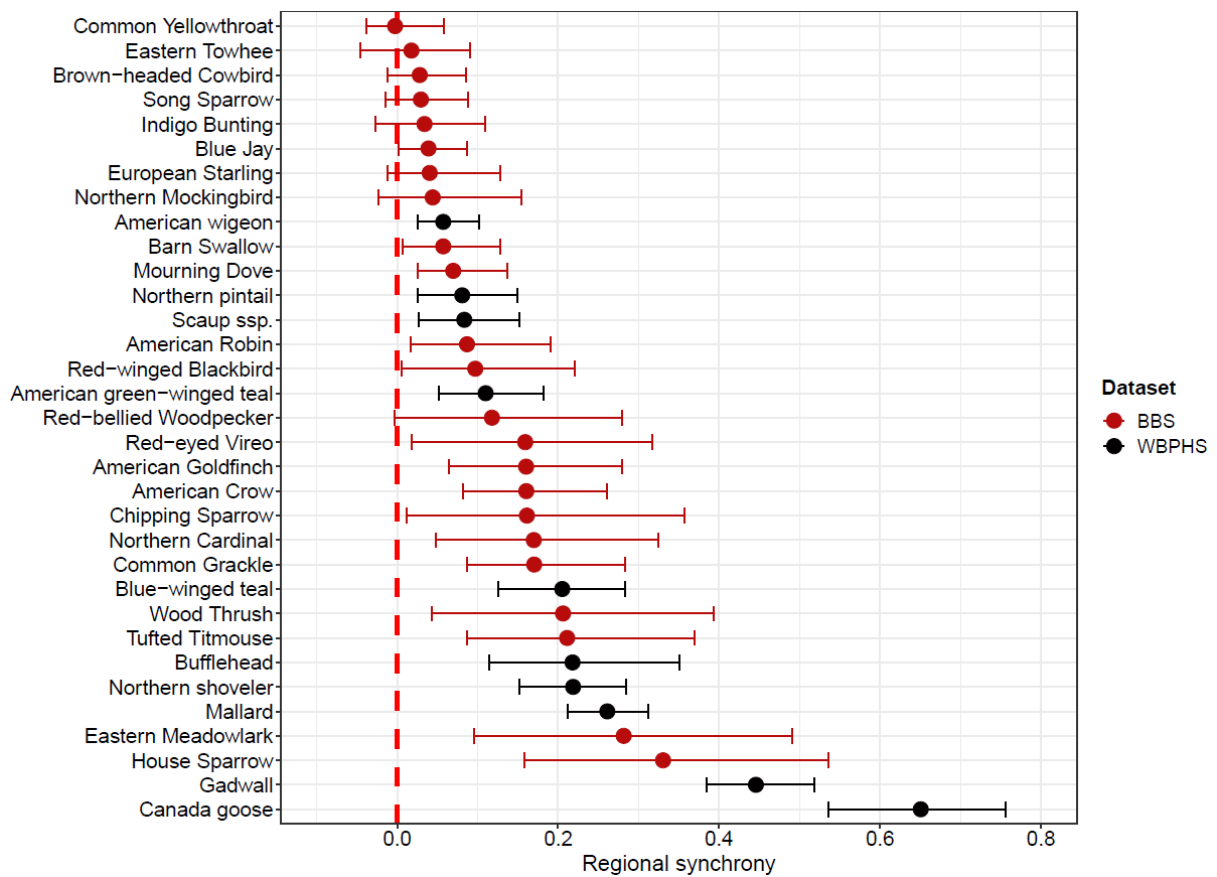
Figure 2: Changes in spatial population synchrony estimated for three different distance intervals for the North American Breeding Bird Survey (BBS) data and Waterfowl Breeding Population and Habitat Survey (WBPHS) data. The points are the estimated spatial population synchrony from the pairwise correlations for all 33 species divided by dataset and distance interval. The linear regressions are the estimated intercepts and slopes from the linear mixed effect model (Table 1). The red line (WBPHS: 500 – 1000 km) has an almost identical slope and intercept as the yellow line (BBS: < 500 km) and was therefore almost hidden by the yellow line.

Table 1: The model output of a linear mixed effect model investigating changes in spatial population synchrony across all species from 1975 to 2019. The estimated spatial population synchrony was the response variable, and the fixed effects were distance intervals with two-way interaction with both time (3-year windows) and dataset, with short distances in WBPHS as intercept. Species was added as a random effect on the intercept and window as a random effect on the slope. The intercept was set to be the value of synchrony calculated from the first window. The parameter estimates are presented with 95% confidence intervals and p-values. P-values lower than 0.05 are regarded as statistically significant and highlighted with bold font.

<b>Change in spatial population synchrony</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>P</i>
Intercept	0.187	0.159 – 0.216	<b>&lt;0.001</b>
Window	-0.002	-0.004 – 0.001	0.237
Intermediate distances	-0.128	-0.164 – -0.092	<b>&lt;0.001</b>
Long distances	-0.206	-0.242 – -0.170	<b>&lt;0.001</b>
BBS	-0.130	-0.156 – -0.104	<b>&lt;0.001</b>
Window * Intermediate distances	0.000	-0.004 – 0.003	0.965
Window * Long distances	0.002	-0.001 – 0.006	0.202
Intermediate distances * BBS	0.112	0.080 – 0.145	<b>&lt;0.001</b>
Long distances * BBS	0.155	0.123 – 0.188	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	1.4*10 <sup>-2</sup>		
$\tau_{00}$ Species	8.5*10 <sup>-4</sup>		
$\tau_{11}$ Species, Window	1.0*10 <sup>-5</sup>		
$\rho_{01}$ Species	-0.83		
ICC	0.03		
N <sub>Species</sub>	33		
Observations	1485		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.144 / 0.171		

There was species-specific variation in the estimated regional synchrony (Fig. 3). However, the majority of the species had either low or no regional synchrony. Gadwall (*Mareca strepera*) and Canada Goose (*Branta canadensis*) had high regional synchrony.

Figure 3: The estimated regional synchrony (i.e. the degree of synchrony across distance) of 33 North American breeding birds. The confidence intervals were based on the 2.5% and 97.5% quantiles. The red colour represents the species from the BBS and the black colour represents the species from the WBPHS.



There was species-specific variation in the change in spatial population synchrony in all distance intervals (Fig. 4 & A1). However, the change in spatial population synchrony was significant only for 6 of 33 species: Red-eyed Vireo (*Vireo olivaceus*) at short, intermediate and long distances, Song Sparrow (*Melospiza melodia*) at short and long distances, European Starling (*Sturnus vulgaris*) at long distances, Northern Pintail (*Anas acuta*) at long distances, Canada Goose at short distances and Wood Thrush (*Hylocichla mustelina*) at long distances. Nonetheless, with a significance level of 0.05, there is a 5% chance of rejecting  $H_0$  (no change in spatial population synchrony) when  $H_0$  is true (type I error). The number of significant trends expected from the significance level is 5, which is close to the 9 significant trends in my analysis.

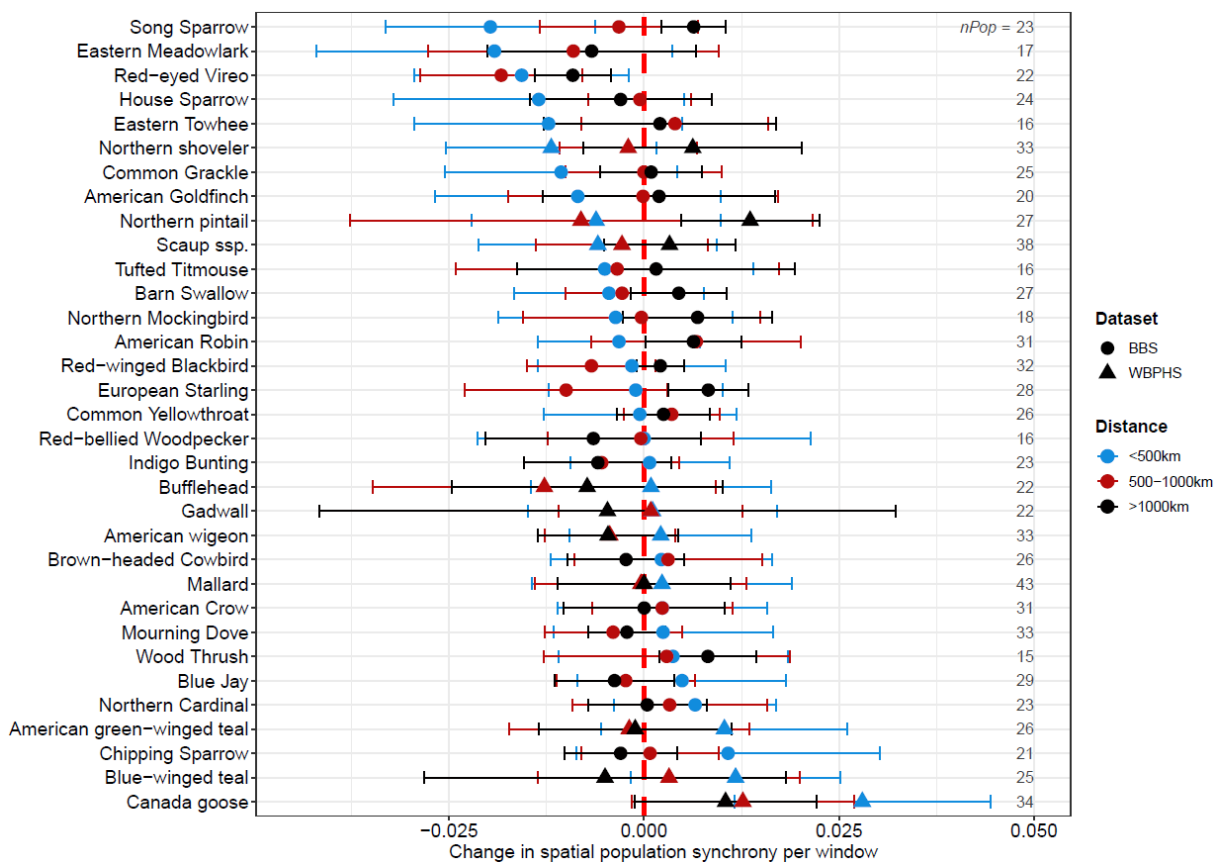


Figure 4: Species-specific temporal trends in spatial population synchrony (estimated change per 3-year window) at different distance intervals. The dots are the estimated effects (slopes) from a linear model with spatial population synchrony as the response variable and 3-year windows as the predictor variable. The lines are the 95% confidence interval for the slope. nPop is the number of populations included in the analysis for each species. The blue dots are the estimates of change among populations that are closer than or equal to 500 km, the red dots are the estimates of change among populations between 500 and 1000 km apart and the black dots are the estimates of change among populations further than 1000 km from each other. Circles represent the BBS and triangles the WBPBS.



I found no evidence of a change in the spatial autocorrelation of mean annual temperature from 1975 to 2019 in neither the BBS region nor the WBPHS region at short, intermediate and long distances. Similar results were found for the spatial autocorrelation of total annual precipitation in the BBS region and WBPHS region at short, intermediate and long distances (Fig. 5 & Table 2)

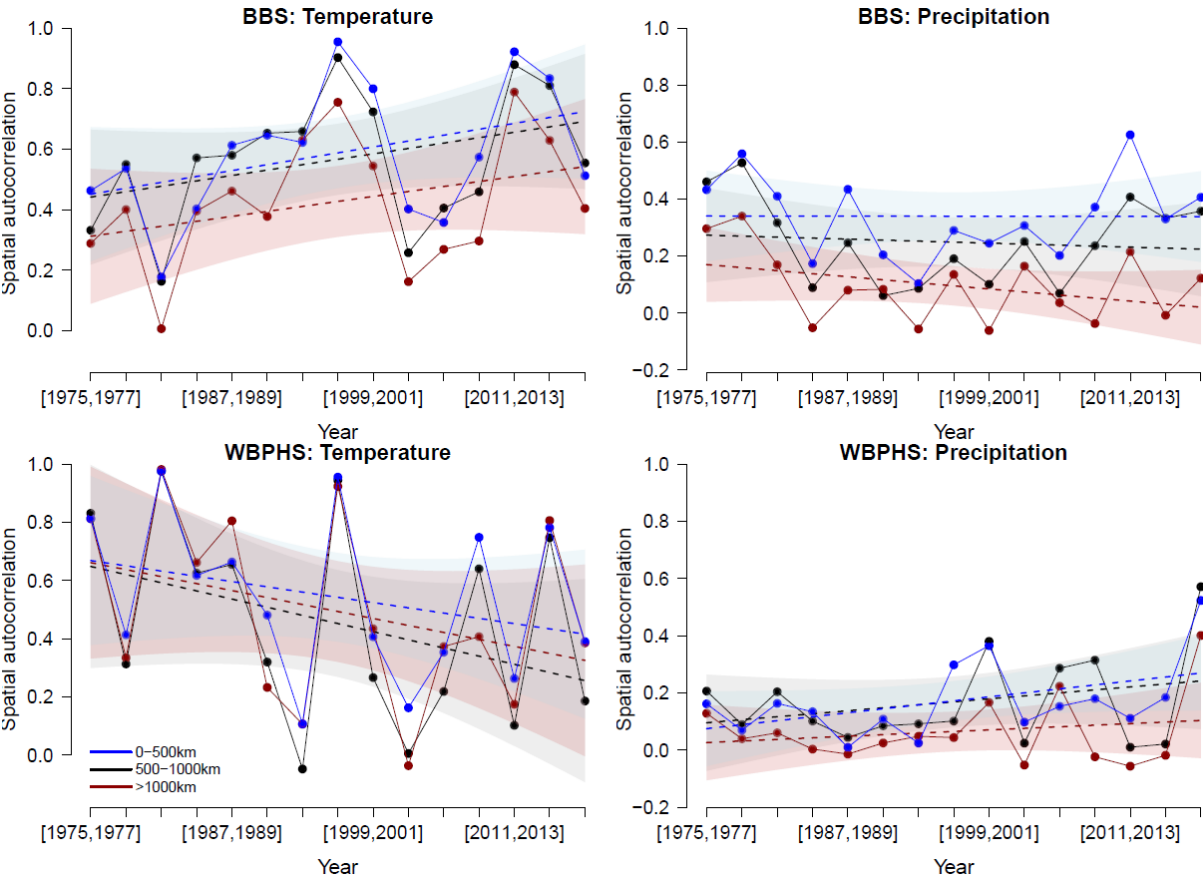


Figure 5: The spatial autocorrelation of mean annual temperature and total annual precipitation in the same regions for the same time period as BBS and WBPHS (Fig 1). The slope and 95% CI are from linear models for each weather variable, region and distance interval with spatial autocorrelation as the response variable and 3-year windows as a predictor variable (Table 2). The blue colour is the sites with a distance of 0 – 500 km, the black colour is the sites with a distance of 500 – 1000 km and the red colour is the sites that are further apart than 1000 km.

Table 2: The change in the spatial autocorrelation of mean annual temperature and total annual precipitation. The slope, standard error (SE) and p-value ( $\alpha = 0.05$ ) of the linear model with the estimated spatial autocorrelation as the response variable and 3-year windows as the predictor variable. The linear model was repeated for each dataset, climatic variable and distance interval (< 500 km, 500 – 1000 km and > 1000 km).

<b>Change in the spatial autocorrelation of environment</b>					
<i>Dataset</i>	<i>Climatic variable</i>	<i>Distance interval</i>	<i>Slope</i>	<i>SE</i>	<i>p</i>
<b>BBS</b>	Temperature	< 500 km	0.019	±0.013	0.148
		500 – 1000 km	0.018	±0.013	0.182
		> 1000 km	0.016	±0.013	0.222
	Precipitation	< 500 km	0.000	±0.009	0.950
		500 – 1000 km	-0.003	±0.009	0.732
		> 1000 km	-0.010	±0.007	0.186
<b>WBPHS</b>	Temperature	< 500 km	-0.007	±0.014	0.674
		500 – 1000 km	-0.013	±0.017	0.441
		> 1000 km	-0.017	±0.019	0.374
	Precipitation	< 500 km	0.013	±0.007	0.095
		500 – 1000 km	0.010	±0.010	0.316
		> 1000 km	0.005	±0.008	0.503

## Discussion

By using long-term time series of population count data, this study found no evidence that the estimated spatial population synchrony across 33 North American bird species has changed from 1975 to 2019. Some species experienced a significant change in spatial population synchrony, but this was expected based on the significance level ( $\alpha = 0.05$ ) and there was no evidence for a change in spatial population synchrony among the majority of species (27 out of 33 species, Fig. 4). Spatial population synchrony was generally higher at short distances (< 500 km) than at intermediate (500 – 1000 km) and long distances (> 1000 km, Table 1 & Fig. 2), which was expected since the degree of spatial population synchrony decreases with increasing distance among sites (Elton, 1924; Moran, 1953).

A high degree of spatial population synchrony is associated with an increased risk of extinction (Heino et al., 1997; Engen et al., 2002). If the estimated spatial population synchrony has not changed over time, it's unlikely that the risk of extinction has increased due to spatial population synchrony for the species used in this analysis. This is good news considering the existing negative impacts on birds such as habitat loss, habitat fragmentation, and climate change but as several other factors can influence extinction risk, species might face extinction without spatial population synchrony changing (Andren, 1994; Brotons & Jiguet, 2010; Dunn et al., 2010; Ambrosini et al., 2019). Despite no strong evidence of changes in spatial population synchrony, there is potential for changes in the future because of climate change and anthropogenic activities (Bellamy et al., 2003; Abbott, 2011; Hansen et al., 2020; Jarillo et al., 2020). Using data from the BBS, Allen and Lockwood (2021) also found no evidence of an overall change in spatial population synchrony across North American grassland bird species. They did, however, find that populations in two specific regions (Prairie Pothole Region and Shortgrass Prairie Region) experienced a significant increase in spatial population synchrony. Furthermore, they found that spatial population synchrony in the eastern United States significantly decreased. Even though the species Allen and Lockwood (2021) studied were different from the species in this study, they highlight that investigating a change in spatial population synchrony at a large spatial scale might hide changes in spatial population synchrony in specific regions at a smaller scale.

Due to lower population variability with increasing latitude, there is geographic variation in the population dynamics of waterfowl (Sæther et al., 2008), and this might explain the low degree of spatial population synchrony I observed since I investigated spatial population synchrony across a large latitudinal gradient. Furthermore, Sæther et al. (2008) suggest that the spatial variation in wetlands can explain the latitudinal gradient of the effect of environmental stochasticity on population dynamics. Additionally, they found that waterfowl at more northern latitudes are less affected by temporal variation in wetlands than in the south. Since I did not account for such latitudinal gradients when estimating spatial population synchrony, there could be undetected changes in spatial population synchrony at lower latitudes where populations are more influenced by changes in environmental variability while at higher latitudes spatial population synchrony remained relatively stable through time.

It is still possible that the spatial population synchrony might have changed over time among more species, but the analysis may have lacked the power to detect it due to noise and sources of error in the datasets (e.g. observation error). Furthermore, the amount of variation explained by the fixed and random effects in the model was low (Table 1). While conducting the BBS, observers' knowledge and experience of counting birds can impact detectability and thus introduce bias, and this was especially prevalent among routes that have changed observers through time (Sauer et al., 1994; Kendall et al., 1996). This observation error was also present in the WBPHS, where the observers' ability to detect individuals differed between species and habitats (Barker, 2015). Consequently, observation error would increase the uncertainty in the counts and decrease the estimated spatial population synchrony of species (Lande et al., 1999). Using more complicated models, such as Bayesian hierarchical models, would help control for sources of error (Bellamy et al., 2003; Abbott, 2011; Hansen et al., 2020; Jarillo et al., 2020) and might be an important step going forward. However, surveys often lack the information necessary to control for observation error. Even when using Bayesian hierarchical models, it can be difficult to eliminate all the observation error and gain unbiased estimates (Lillegård et al., 2008). Nevertheless, using more complicated models to account for sources of error when possible, can decrease the uncertainty of the results.

The populations were aggregated at the state and province level (for BBS) and stratum level (for WBPHS) to increase the population count per site and thus reduce the demographic stochasticity that is evident in low population counts. However, the aggregation also reduced my sample size which could increase the probability of accepting  $H_0$  (no change in spatial

population synchrony) when  $H_1$  was true (type II error). Problems with observation error, data quality, length of time series, survey method and sampling discontinuity are common in population-dynamic studies (Yoccoz et al., 2001), as well as when analysing spatial population synchrony (Bjørnstad et al., 1999; Santin-Janin et al., 2014). Gathering data that have long time series, low sources of error and are of good quality are time-consuming, expensive and difficult. This further cements the difficulties with precisely and accurately estimating spatial population synchrony.

Although there was species-specific variation in the estimated regional synchrony, the majority had either low or no regional synchrony (Fig. 3). Comparing the six species that experienced a significant change in spatial population synchrony (Red-eyed Vireo, Song Sparrow, European Starling, Northern Pintail, Canada Goose and Wood Thrush) with their regional synchrony, only Canada Goose had high regional synchrony. Among the six species, it did not seem like there was any clear pattern between regional synchrony and a significant change in spatial population synchrony. However, it's important to note that the estimated regional synchrony was not divided into distance intervals which was the case for changes in spatial population synchrony.

Red-eyed Vireo had low regional synchrony (Fig. 3) and was the only species with a significant change in spatial population synchrony over short, intermediate, and long distances (Fig. 4). Red-eyed Vireo is sensitive to forest fragmentation, likely due to lower fledging success because of the increasing rate of brood parasitism with less forest cover (Donovan et al., 1995; Robinson & Robinson, 1999; Burke & Nol, 2000). Furthermore, habitat fragmentation is likely to increase due to climate change and anthropogenic activities (Fischer & Lindenmayer, 2007; Bennett & Saunders, 2010; McKelvey et al., 2011; Post et al., 2013) and can potentially drive changes in spatial population synchrony (Bellamy et al., 2003). Therefore, this species might be of interest for further research.

The shortest distance interval tested was 0 – 500 km. However, habitats 500 km apart can encompass large topographic differences as well as differences in the environment and its effect on population dynamics (Qian et al., 2009). Furthermore, spatial population synchrony can decrease rapidly with increasing distance. Subsequently, the distance interval of 0 – 500 km might be too large, and, for instance, the degree of spatial population synchrony might be higher at sites 250 km apart or lower. However, the number of pairwise correlations between sites 0 –

250 km apart was lower than my criteria of 10 for all my species and thus the distance interval was excluded from the analysis.

My lack of evidence for an overall temporal trend in spatial population synchrony across bird species deviated from some previous findings in single-species studies: Caribou (Post & Forchhammer, 2004), Gypsy Moth (*Lymantria dispar*; Allstadt et al., 2015) and Glanville Fritillary Butterfly (Tack et al., 2015; Kahilainen et al., 2018). All of these species belonged to different taxonomic classes than birds and thus likely have different ecological requirements. Hence, changes in the environment might affect the population dynamics of these species differently. Moreover, the studies mentioned are single-species studies which have the advantage of incorporating species-specific details in the models. It's therefore not necessarily surprising that my results differed from theirs.

In contrast to my results, Koenig and Liebhold (2016) found a general increase in spatial population synchrony among 49 North American bird species. This increase was observed at distance intervals of 0 – 250 km, 250 – 500 km and 500 – 1000 km. Importantly, they analysed only species that were significantly synchronous at short distances (250 – 500 km), while I analysed species based on a minimum number of pairwise populations in each distance interval and therefore was investigating changes in spatial population synchrony regardless of their degree of spatial population synchrony. The criteria used by Koenig and Liebhold (2016) for inclusion could result in a larger proportion of species with an observed change in spatial population synchrony, which could explain the difference in the results. They analysed 49 species from the North American Christmas Bird Count (CBC) and 8 of these species (American Goldfinch [*C. brachyrhynchos*], American Robin [*T. migratorius*], Blue Jay [*C. cristata*], European Starling, Mourning Dove [*Z. macroura*], Northern Cardinal [*C. cardinalis*], Northern Mockingbird [*M. polyglottos*] and Song Sparrow) overlapped with the species I analysed, which all were from the BBS. I compared the species at the distance interval of 0 – 500 km and 500 – 1000 km, and 6 of the 8 species (American Goldfinch, American Robin, Blue Jay, Mourning Dove, Northern Mockingbird, Song Sparrow) showed similar trends in the spatial population synchrony at one or both distance intervals. However, Koenig and Liebhold (2016) did not provide the statistical significance for the changes in spatial population synchrony for each species and therefore it was difficult to determine how similar or dissimilar the trends were. Among the species and distance intervals compared with Koenig and Liebhold,

only Song sparrow experienced a significant change in spatial population synchrony in my analysis (Fig. 4).

As opposed to Koenig and Liebhold (2016), I found no evidence of a change in the spatial autocorrelation of mean annual temperature (Fig. 5, Table 2), a weather variable that can be assumed to directly or indirectly drive changes in spatial population synchrony through, for instance, effects on growth rates, carrying capacity and dispersal rate (Sæther et al., 2000; Pärn et al., 2012; Hansen et al., 2019b). Furthermore, considering previous research indicates a change in the spatial autocorrelation of temperature (Koenig, 2002; Post & Forchhammer, 2004; Allstadt et al., 2015; Di Cecco & Gouhier, 2018; Dallas et al., 2020), it was surprising that I found no evidence for that change. One reason for this could be that the weather data was aggregated to match the size and location of the strata, states and provinces used in the analysis of the bird species. This was mainly done because I was not able to gather individual weather station data for the U.S that fulfilled the criteria of having data every year from 1975 to 2019. Another reason might be because of the different data and geographic coverage analysed. Furthermore, several of the studies indicating changes in the spatial autocorrelation of temperature analysed time series spanning more than 100 years (Koenig, 2002; Post & Forchhammer, 2004; Allstadt et al., 2015; Di Cecco & Gouhier, 2018), which is over double the length I analysed. The aggregation of the weather data reduced the sample and could reduce the statistical power to detect changes in spatial synchrony and increase the chance of type II error. The lack of evidence for changes in spatial autocorrelation of precipitation was somewhat expected since Koenig and Liebhold (2016) had not observed a change in the spatial autocorrelation of precipitation in a similar geographical area.

The global temperature is projected to increase in the coming decades due to climate change but the increase will likely vary with season and latitude (IPCC, 2021). IPCC (2021) further reports that, for instance, at high latitudes climate change has greater effects on winter temperatures than summer temperatures. Consequently, annual weather variables (e.g. annual temperature and precipitation) might not capture these changes and thus changes in seasonal weather variables (e.g. winter temperature and spring precipitation) may be better explanatory variables. Furthermore, changes in seasonal weather variables might be more influential on the population dynamics of some species (Schaefer et al., 2008; Sæther et al., 2008; Kanno et al., 2016; Woodworth et al., 2017). However, when analysing multiple species with different ecological requirements and species-specific responses to the environment, the species likely



have different seasonal weather variables that could explain changes in population dynamics. Therefore, choosing a set of seasonal variables may be difficult. Although annual weather variables might not give the full picture of all key environmental variables, they can be reasonable substitutes when investigating multiple species. Nevertheless, for future studies it might be better to both analyse annual weather variables as well as key seasonal weather variables.

An increased rate of dispersal among populations has a positive effect on spatial population synchrony (Ranta et al., 1997b; Paradis et al., 1999) and if the rate of dispersal changes over time, e.g. due to climate change (Figuerola, 2007; McKelvey et al., 2011; Pärn et al., 2012), it can potentially induce a change in spatial population synchrony. Similarly, a change in the effect of species interactions (e.g. predator-prey interactions) would likely influence the spatial population synchrony over time (Figuerola, 2007; McKelvey et al., 2011; Pärn et al., 2012). The rate of dispersal and species interaction are often species-specific and can vary both temporally and spatially (Nathan, 2001; Rooney et al., 2008; Urban et al., 2013; Pellissier et al., 2018). Therefore, the magnitude and direction of a potential change in these mechanisms may vary among species and subsequently potential changes in spatial population synchrony may also vary.

There are several different approaches for analysing changes in spatial population synchrony (e.g. inverse coefficient of variation, correlogram and moving windows; Post & Forchhammer, 2004; Defriez et al., 2016; Koenig & Liebhold, 2016). However, Le Moullec et al. (2021) found that the approaches varied in the ability to detect a true change in spatial population synchrony and the precision of the results. Of all the approaches currently in use, a moving window analysis with short nonoverlapping window sizes was determined to have the highest detectability and precision for analysing data on 20 populations spanning 50 years. The simulations from Le Moullec et al. (2021) assumed no observation error and that was not the case for the WBPHS (Barker, 2015) and BBS data (Sauer et al., 1994; Kendall et al., 1996). Observation error would increase the variance in the estimated population size but is not expected to influence the covariance among independent populations (Lande et al., 1999). Consequently, the estimated spatial population synchrony tends to be lower when observation error is high/not accounted for. Therefore, the optimum window length and degree of overlap might be different if observation error was accounted for in the simulations. Le Moullec and colleagues (in prep.) are currently developing a new method based on a multivariate normal



distribution that will enhance the detectability of a true change in spatial population synchrony compared to the other methods. Accordingly, the approach chosen can greatly influence the estimated change in spatial population synchrony.

There is a trade-off between studying single species and multiple species. Studying single species allows you to tailor the models to deal with data issues in that particular species and detailed information about its population dynamics and ecological requirements can be incorporated. However, it's difficult to extend the conclusion to other species and find general patterns. Multispecies studies are more suited for investigating general patterns but at the expense of incorporating detailed ecological variables in the model because of large ecological differences among species. Choosing groups of species with relatively similar ecological requirements, such as waterfowl with their common dependence on wetland dynamics (this thesis), incorporates some of the benefits from both single and multispecies studies.

In conclusion, I found no evidence of an overall change in spatial population synchrony among the 33 North American bird species analysed. There were, however, noise and sources of error in the datasets that could have influenced the results. Similarly, there was no evidence of a change in the spatial autocorrelation of temperature and precipitation. Considering the amount of previous research indicating the spatial autocorrelation of temperature has changed over time (Koenig, 2002; Post & Forchhammer, 2004; Allstadt et al., 2015; Koenig & Liebhold, 2016; Di Cecco & Gouhier, 2018; Dallas et al., 2020), it's possible the analysis was not able to detect a change. Considering the change and degree of spatial population synchrony can give valuable insight into the extinction risk of species, these studies are important for allocating conservation efforts, especially considering the Earth is entering its sixth mass extinction event (Ceballos et al., 2015). There, however, are often data quality challenges when analysing population count data which makes it difficult to estimate trends in spatial population synchrony accurately and precisely. Nevertheless, there is still a need for more multispecies studies (similar to this study) to better understand if changes in spatial population synchrony are more species-specific or general across "similar" groups of species.

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## Appendix

Table A1: Common name, scientific name and corresponding dataset for each species used in the analysis.

Common name	Scientific name	Dataset
American Crow	<i>Corvus brachyrhynchos</i>	BBS
American Goldfinch	<i>Spinus tristis</i>	BBS
American Green-winged Teal	<i>Anas carolinensis</i>	WBPHS
American Robin	<i>Turdus migratorius</i>	BBS
American Wigeon	<i>Mareca americana</i>	WBPHS
Barn Swallow	<i>Hirundo rustica</i>	BBS
Blue Jay	<i>Cyanocitta cristata</i>	BBS
Blue-winged Teal	<i>Spatula discors</i>	WBPHS
Brown-headed Cowbird	<i>Molothrus ater</i>	BBS
Bufflehead	<i>Bucephala albeola</i>	WBPHS
Canada Goose	<i>Branta canadensis</i>	WBPHS
Chipping Sparrow	<i>Spizella passerina</i>	BBS
Common Grackle	<i>Quiscalus quiscula</i>	BBS
Common Yellowthroat	<i>Geothlypis trichas</i>	BBS
Eastern Meadowlark	<i>Sturnella magna</i>	BBS
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	BBS
European Starling	<i>Sturnus vulgaris</i>	BBS
Gadwall	<i>Mareca strepera</i>	WBPHS
House Sparrow	<i>Passer domesticus</i>	BBS
Indigo Bunting	<i>Passerina cyanea</i>	BBS
Mallard	<i>Anas platyrhynchos</i>	WBPHS
Mourning Dove	<i>Zenaida macroura</i>	BBS
Northern Cardinal	<i>Cardinalis cardinalis</i>	BBS
Northern Mockingbird	<i>Mimus polyglottos</i>	BBS
Northern Pintail	<i>Anas acuta</i>	WBPHS
Northern Shoveler	<i>Spatula clypeata</i>	WBPHS
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	BBS
Red-eyed Vireo	<i>Vireo olivaceus</i>	BBS
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	BBS
Scaup ssp.	<i>Aythya marila</i> & <i>Aythya affinis</i>	WBPHS
Song Sparrow	<i>Melospiza melodia</i>	BBS
Tufted Titmouse	<i>Baeolophus bicolor</i>	BBS
Wood Thrush	<i>Hylocichla mustelina</i>	BBS

Figure A1: The estimated spatial population synchrony of North American bird species from the WBPHS and the BBS, using data from 1975 to 2019 with the moving windows approach. The slope and 95% CI were from linear models with spatial population synchrony as the response variable and 3-year windows as the predictor variable for each species and distance interval. Sites that were 0 – 500 km apart are in blue, 500 – 1000 km are black, and > 1000 km apart are red.

