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Temporally increasing spatial synchrony of North American temperature and bird populations

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The ecological impacts of modern global climate change are detectable in a wide variety of phenomena, ranging from shifts in species ranges to changes in community composition and human disease dynamics[1-3]. So far, however, little attention has been given to temporal changes in spatial synchrony—the coincident change in abundance or value across the landscape[4]—despite the importance of environmental synchrony as a driver of population trends and the central role of environmental variability in population rescue and extinction[1,5,6]. Here we demonstrate that across North America, spatial synchrony of a significant proportion of 49 widespread North American wintering bird species has increased over the past 50 years—the period encompassing particularly intense anthropogenic effects in climate—paralleling significant increases in spatial synchrony of mean maximum air temperature. These results suggest the potential for increased spatial synchrony in environmental factors to be affecting a wide range of ecological phenomena. These effects are likely to vary, but for North American wildlife species, increased spatial synchrony driven by environmental factors may be the basis for a previously unrecognized threat to their long-term persistence in the form of more synchronized population dynamics reducing the potential for demographic rescue among interacting subpopulations.

The quest to understand mechanisms driving the dynamics of natural populations has been a key motivation for plant and animal population studies for over a century. Among the more intriguing patterns exhibited by a wide range of taxa is spatial synchrony—the coincident change in abundance (or other time-varying character) of geographically disjunct populations[4]. Spatial synchrony is widespread among ecological phenomena and can be driven by a variety of factors, including dispersal[7], mobile predators[8,9], and environmental drivers (the Moran effect; refs 10,11). It is also thought to play an important role in metapopulation dynamics, primarily because increased synchrony among interacting populations reduces the probability that poorly performing populations can be demographically rescued by emigrants from successful populations, thus increasing the threat of extinction[5,6,12,13]. Consequently, it is of considerable importance to measure the degree to which spatial synchrony is changing as well as whether such changes can be attributed to specific environmental patterns[14,15].

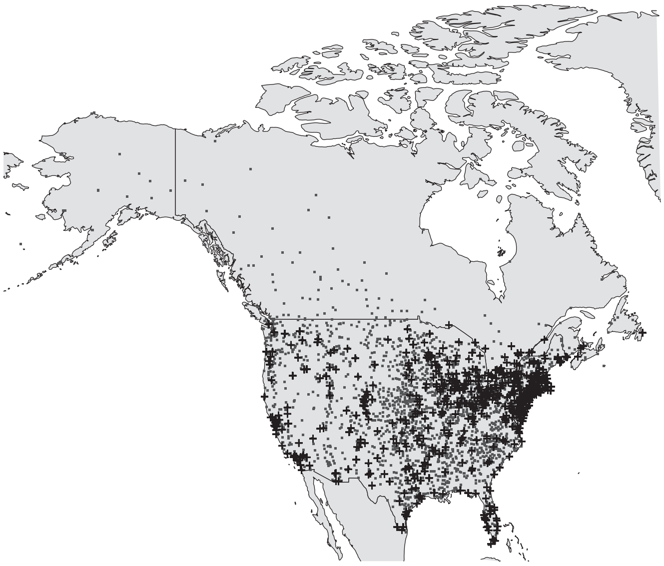

Figure 1 | Locations of North American bird survey sites and weather stations used in the analyses of spatial synchrony. Black crosses are sites of Christmas Bird Count circles ($N \approx 550$ sites) and grey dots are sites providing 40 or more years of temperature ($N \approx 1{,}350$) and/or rainfall ($N \approx 1{,}005$) data between 1960 and 2009.

Here we address this question using 50 years of wintering bird and environmental data from a large number of sites across North America measured between 1960 and 2009 (Fig. 1). We first examined a subset of 49 widespread wintering North American bird species, within each of which significant spatial synchrony had been previously detected[16], to test for temporal changes in synchrony. Analyses were conducted by testing for spatial synchrony among five-year time periods, each of which overlapped the next by two years (16 time periods altogether between 1960–1964 and 2005–2009). We then analysed for parallel temporal trends among temperature and rainfall, which are the most ubiquitous drivers (directly or indirectly) of spatial synchrony on population dynamics[11,17], to determine if synchrony in these environmental parameters changed in parallel with those detected among the bird species. Previous analyses indicate that both temperature and rainfall are spatially synchronous between sites separated by up to 1,000–2,500 km in North America as well as in other regions globally[17], but neither temporal changes in spatial synchrony of environmental factors nor their potential effects on the population dynamics of animal populations have been previously investigated on a continental scale.

During the 50-year study period, spatial synchrony increased in 63–69% of the 49 bird species among sites <1,000 km

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Table 1 | Temporal changes in spatial synchrony among 49 widespread species of North American birds and correlations between mean spatial synchrony of the birds and mean maximum annual temperature (lagged by one time period).

	50-year trend in spatial synchrony				Correlation between mean spatial synchrony of birds and spatial synchrony of mean maximum annual temperature (lagged)	
Distance category	*N* species positive	*N* species non-positive	Percentage species positive	*P*-value*	*r*-value	*P*-value
0–250 km	34	15	69.4	0.009	0.56	0.029
250–500 km	31	18	63.3	0.09	0.53	0.040
500–1,000 km	32	17	65.3	0.04	0.44	0.099
1,000–2,500 km	27	22	55.1	0.39	−0.08	0.79
2,500–5,000 km	24	25	49.0	1.00	−0.28	0.30

*Binomial test.

Table 2 | Temporal change in North American meteorological spatial synchrony, 1960–1964 to 2005–2009.

			Overall mean spatial synchrony (with trend per decade, 1960–1964 to 2005–2009)				
Variable	Time period	Mean ± standard error trend of variable (in standard deviations)†	<250 km	250–500 km	500–1,000 km	1,000–2,500 km	2,500–5,000 km
Mean max. temp.	Annual	+2.86 ± 0.65***	0.790 (**+0.031****)	0.718 (**+0.044****)	0.569 (**+0.065****)	0.284 (**+0.091*****)	0.010 (+0.041)
Mean max. temp.	Summer	+1.89 ± 0.31***	0.814 (**+0.034****)	0.712 (+0.040)	0.514 (+0.038)	0.161 (+0.033)	−0.102 (−0.016)
Mean max. temp.	Winter	+4.76 ± 1.35**	0.899 (+0.005)	0.825 (+0.006)	0.668 (+0.013)	0.374 (+0.007)	0.017 (−0.008)
Mean min. temp.	Annual	+3.08 ± 0.29***	0.711 (+0.020)	0.657 (+0.025)	0.533 (+0.040)	0.254 (+0.074)	0.008 (+0.490)
Mean min. temp.	Summer	+2.80 ± 0.11***	0.675 (**+0.024***)	0.602 (**+0.031***)	0.446 (**+0.042***)	0.108 (+0.038)	−0.031 (−0.012)
Mean min. temp.	Winter	+5.17 ± 0.96***	0.871 (+0.007)	0.808 (+0.010)	0.664 (+0.020)	0.341 (+0.043)	−0.021 (+0.049)
Rainfall	Annual	−4.48 ± 13.14	0.604 (−0.003)	0.402 (−0.014)	0.213 (−0.027)	0.052 (−0.029)	0.026 (−0.005)
Rainfall	Summer	+2.57 ± 1.88	0.470 (+0.028)	0.263 (+0.027)	0.109 (+0.007)	0.002 (−0.006)	−0.049 (−0.008)
Rainfall	Winter	−2.29 ± 6.40	0.683 (−0.001)	0.445 (−0.010)	0.225 (−0.029*)	0.062 (−0.015)	0.021 (+0.011)

†Analyses involved moving windows of time, each of which was five years in length separated by three years (16 time windows in total). Significance of the overall trends in temperature and rainfall are based on the Cochrane–Orcutt procedure adjusting for temporal autocorrelation. For all analyses, the minimum number of years for a site to be included was 40. Summer, June–August; winter, January–March. *N* sites ranged from 1,053 to 1,932. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; significant increases in spatial synchrony are highlighted in bold. All overall mean spatial synchrony values were significantly greater than zero except the 1,000–2,500 km distance category for summer rainfall and the 2,500–5,000 km distance category for annual mean maximum temperature and annual mean minimum temperature.

apart, proportions that were significant for sites <250 km and 500–1,000 km apart (summary in Table 1; details in Supplementary Table 1). Averaging mean spatial synchrony values across all 49 species, values exhibited possible cyclic behaviour, and there was considerable temporal variability (Fig. 2). We found no significant differences based on the migratory status of the birds involved (Kruskal–Wallis analysis of variance (ANOVA), all $P > 0.05$).

Parallel analyses were performed on North American temperature and precipitation to determine if these environmental drivers could be responsible for these results. Analyses confirmed that mean temperatures increased during the 1960–2009 period, more so during the boreal winter than the boreal summer, whereas no significant temporal trends in rainfall were detected (Table 2). As found in previous analyses[17], spatial synchrony was significantly positive in virtually all analyses between sites <2,500 km apart and was generally greater for temperature than rainfall. Spatial synchrony between sites 2,500 and 5,000 km apart was in some cases significantly negative, suggesting inverse east coast versus west coast environmental dynamics, comparable to dipoles that have been identified as being important drivers of boreal bird irruptions[18].

Over the same 50-year time period encompassed by the bird data, our analyses revealed significant and relatively striking increases in meteorological spatial synchrony across all but the largest 2,500–5,000 km spatial scale in mean maximum temperature (Table 2); significant increases were also indicated by temporal patterns in the regional average spatial correlation and the estimated maximum extent of spatial synchrony (Fig. 3). Increases were mainly observed during the boreal summer, whereas no significant increases in spatial synchrony during the boreal winter were detected, despite increases in mean absolute temperature even greater than those observed during the summer (Table 2). Changes in spatial synchrony between 1960–1964 and 2005–2009 were modest at short distances where spatial synchrony was initially high, but were greater at longer distance categories, even switching from being significantly negative to significantly positive between sites 2,000 and 5,000 km apart (Fig. 4). Changes in spatial synchrony in mean minimum temperatures were similar to those of mean

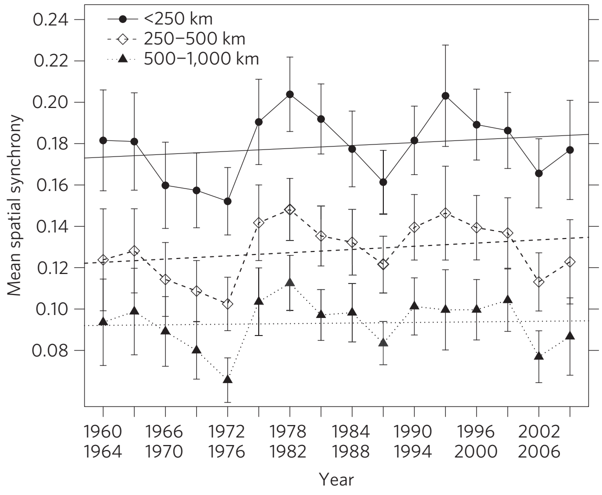

Figure 2 | Overall spatial synchrony for 49 North American wintering bird species. Values plotted are the means ± standard errors for three spatial scales (sites 0–250 km apart, 250–500 km apart and 500–1,000 km apart) for each 5-year time window, starting from 1960–1964 and ending with 2006–2010, along with the linear trend lines.

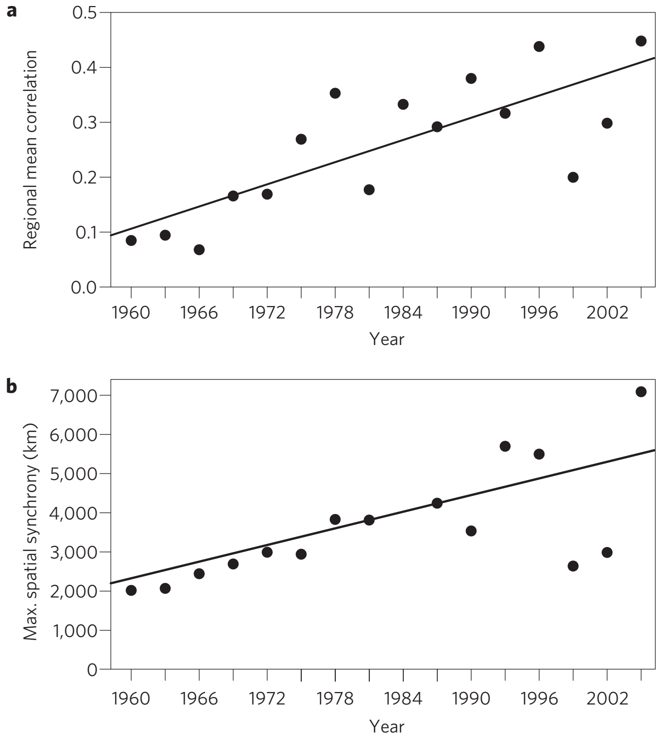

Figure 3 | Overall change in spatial synchrony of mean maximum temperature across North America, 1960–2009. a, Regional average spatial synchrony, as estimated by nonparametric spatial covariance functions at each time interval[29], plotted against year; regression coefficient (± standard error) estimated by the Cochrane–Orcutt procedure $= 0.0064 \pm 0.0015$, $t = 4.34$, $P < 0.001$. **b**, Maximum extent of spatial synchrony, as estimated by the nonparametric spatial covariance function[29], plotted against year; regression coefficient (± standard error) estimated by the Cochrane–Orcutt procedure $= 67.2 \pm 31.4$, $t = 2.14$, $P = 0.05$.

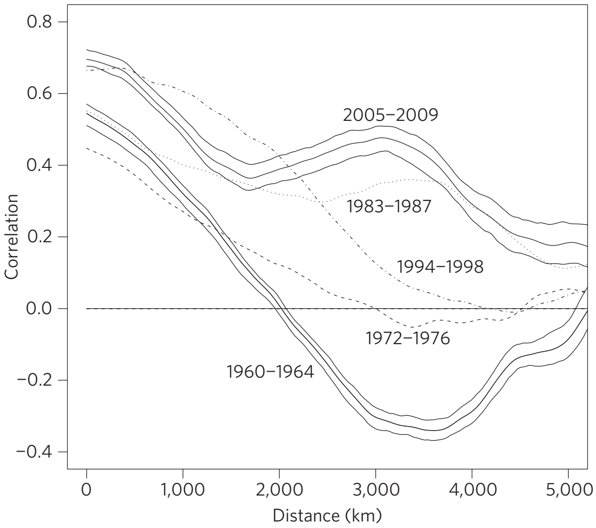

Figure 4 | Temporal change in spatial synchrony in North American annual mean maximum temperature. Values plotted are mean r-values (mean spatial synchrony) for sites separated by 0–5,000 km using nonparametric spatial covariance functions[30,31] for five 5-year time periods: 1960–1964, 1972–1976 (dashed line), 1983–1987 (dotted line), 1994–1998 (dot-dashed line) and 2005–2009. Only the mean values are plotted, except for the first (1960–1964) and last (2005–2009) time periods, for which both means and 95% confidence intervals are shown.

maximum temperature in that observed increases were observed primarily during the boreal summer; however, overall increases were not statistically significant. Temporal changes in precipitation synchrony were variable (positive during the boreal summer; negative during the boreal winter) and were generally not significant over the time period analysed (Supplementary Figs 1–3).

Across the 16 five-year overlapping time periods, we found no significant correlations between the mean spatial synchrony of the 49 bird populations and spatial synchrony of mean maximum annual temperature. However, significant positive correlations ($P < 0.05$) were found between these variables for spatial scales <500 km when mean maximum annual temperatures were lagged by one time period (Table 1). These results are thus consistent with the hypothesis that increased spatial synchrony in temperature is at least one factor that is driving the increase in spatial synchrony of wintering bird populations observed after a lag of a few years.

Among the 49 wintering North American bird species analysed, spatial synchrony in numbers has generally increased over a 50-year time period (1960–2009) between sites up to 1,000 km apart, an increase that is potentially being driven in part by previously undetected increases in spatial synchrony in temperature that have taken place parallel with the well-documented increases in global temperatures during recent decades[19]. Increases in synchrony have been strongest in mean maximum temperatures during the boreal summer and have been less striking for mean minimum temperature and during the boreal winter; no significant temporal trends in spatial synchrony in precipitation were detected. Although previous studies have demonstrated significant spatial synchrony in environmental conditions on large geographic scales worldwide[17], we are aware of no previous study that has investigated temporal changes in spatial synchrony among animal populations or in environmental factors on a continental scale.

Further analyses are needed to test whether the causes of the observed changes are due to large-scale climatic perturbations such as the North Atlantic or El Niño–Southern Oscillations, both of which have increased in frequency or variability in recent decades in parallel with observed increases in spatial synchrony[20–22]. Ultimately, however, global climate change is a likely root cause of the increased spatial synchrony in North American temperatures inasmuch as warming over the past several decades has been implicated as a driver of more extreme behaviour in these climate indices[20]. The drivers of the apparent increase in spatial synchrony observed in the bird populations are likely to be more diverse; the lack of any relationship with migratory status suggest no overall strong effect of dispersal, but the heterogeneous nature of the species considered render it likely that multiple ecological factors, including not only the Moran effect but dispersal and mobile predators, may be contributing to patterns of spatial synchrony found in particular species.

Climate plays a key role in driving many population processes in both plants and animals[4,23,24], and thus the increase in spatial synchrony in temperature found here is a potentially important factor driving increased spatial synchrony in other ecological phenomena. Of particular relevance to bird species considered here, spatial synchrony among metapopulations plays a critical role in the potential for population rescue and the probability of extinction, with extinction being more likely as synchrony between geographically disjunct populations increases[5,6,13,25–27]. The significant increase in environmental synchrony reported here is thus a previously unrecognized factor potentially threatening the long-term persistence of species whose survival is dependent on occasional rescue by dispersers from demographically asynchronous populations producing dispersers[26,28,29]. The increases in spatial synchrony detected among the bird species examined demonstrate the potential for such environmental patterns to affect animal populations in subtle ways that have potentially important affects on their prospects for long-term persistence.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

W.D.K. conducted the data analysis; A.M.L. provided critical advice regarding the approach and analyses. Both authors contributed to writing the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to W.D.K.

Competing financial interests

The authors declare no competing financial interests.

Methods

Bird population data. We tested for changes in spatial synchrony among the 49 wintering bird species (Supplementary Table 1) that were found to be significantly synchronous at the 250–500 km spatial scale in an earlier study[16], thereby focusing on species that are geographically widespread and avoiding bias favouring species that exhibit very low (or no) spatial synchrony. Of the 49 species, 11 were residents (nonmigratory), 28 were partial migrants, and 10 were migratory. Analyses were conducted using data from the North American Christmas Bird Count (CBC) program[32] spanning 50 years from 1960 (the 1959–1960 CBC) to 2009 (the 2008–2009 CBC); only sites with at least 40 years of data during this period were included. For each species, all possible pairs of sites were binned into five distance categories (<250 km, 250–500 km, 500–1,000 km, 1,000–2,500 km and 2,500–5,000 km apart). Analyses were performed on relative population numbers as indexed by birds per party hour; Pearson correlations were calculated and then averaged between all pairwise combinations of sites[16,17]. To quantify temporal changes in spatial synchrony, we analysed moving windows of time between 1960 and 2009, each of which was five years in length, separated by three years.

To test for trends in spatial synchrony, we fitted a linear model to the time series for each species x distance category; slopes of the models and significance of trends for the individual analyses were determined by linear regressions of mean spatial synchrony on time (Supplementary Table 1). For overall trends we compared the number of species within each distance category that increased in spatial synchrony over the 50-year time period of the study (as determined by a positive slope of the regression of mean synchrony on time) with the number of species whose overall spatial synchrony decreased during the 50-year time period using binomial tests. Differences between species with different migratory habits were tested using Kruskal–Wallis one-way ANOVAs.

Weather data. Mean monthly precipitation, mean maximum temperature and mean minimum temperature for North America from 1960 to 2009 were obtained from the Global Historical Climate Network[33]. Values were averaged (temperature) or summed (precipitation) across all months in calendar years for annual values, for January through March for the boreal winter, and for June through August for the boreal summer. Years and seasons with missing values were excluded; as with the bird data, final analyses were restricted to sites with 40 or more years of data from 1960 to 2009, inclusive (80% of all years).

Spatial synchrony of weather. Pairs of sites were binned into the same five distance categories used for the bird data (sites <250 km, 250–500 km, 500–1,000 km, 1,000–2,500 km and 2,500–5,000 km apart), and within each distance category synchrony (estimated by Pearson correlation coefficients) was calculated and then averaged between all pairwise combinations of sites[17]. Statistical significance was determined using standard errors estimated from 100 bootstrap trials, each of which included a set of randomly chosen pairwise correlation coefficients that included each individual site only once.

To quantify temporal changes in meteorological spatial synchrony, we again analysed five-year moving windows of time between 1960 and 2009 separated by three-year intervals for a total of 16 intervals (1960–1964 to 2005–2009). Changes in (absolute) mean temperature and rainfall through time were expressed in terms of standard deviations of the mean of the first (1960–1964) time interval. Analyses of these overlapping series indicated significant lag-1 autocorrelations, which we adjusted for in correlation analyses using the Cochrane–Orcutt procedure[34]. Relationships of spatial synchrony of mean maximum annual temperature with changes in mean spatial synchrony of the 49 bird species was analysed by correlating (using the Cochrane–Orcutt procedure to adjust for temporal autocorrelation) values measured both during the same time period and lagged one time period (that is, mean spatial synchrony of the birds during 5-year time period x with that of temperature during 5-year period $x-1$).

Changes in spatial synchrony of temperature and rainfall through time were visualized with nonparametric spatial covariance functions[30] from which we obtained the regional average spatial correlation for each time period and the shortest distance at which the spatial covariance function was estimated to reach 0 (the latter an estimate of the maximum extent of spatial synchrony). We tested these values for correlation with time, again adjusting for temporal autocorrelation using the Cochrane–Orcutt procedure.

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