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DR ALEKSI LEHIKOINEN (Orcid ID : 0000-0002-1989-277X)

MR ANDREA SANTANGELI (Orcid ID : 0000-0003-0273-1977)

DR ALISON JOHNSTON (Orcid ID : 0000-0001-8221-013X)

DR ADAM SMITH (Orcid ID : 0000-0002-2829-4843)

Corresponding Author Email ID: aleksi.lehikoinen@helsinki.fi

Wintering bird communities are tracking climate change faster than breeding communities

Running head: winter and breeding communities and climate

Aleksi Lehikoinen[1], Åke Lindström[2], Andrea Santangeli[1], Päivi M. Sirkiä[1], Lluis Brotons[3,4,5], Vincent Devictor[6], Jaanus Elts[7,8], Ruud P.B. Foppen[9,10,11], Henning Heldbjerg[12,13], Sergi Herrando[3, 14], Marc Herremans[15], Marie-Anne R. Hudson[16], Frédéric Jiguet[17], Alison Johnston[18,19], Romain Lorrilliere[17,20], Emma-Liina Marjakangas[1], Nicole L. Michel[21], Charlotte M. Moshøj[13], Renno Nellis[22], Jean-Yves Paquet[23], Adam C. Smith[16], Tibor Szép[24, 25], Chris van Turnhout[9,10]

[1] Finnish Museum of Natural History, University of Helsinki, Finland.

[2] Department of Biology, Biodiversity unit, Lund University, Ecology Building, S-223 62 Lund, Sweden.

[3] *CREAF, 08193 Cerdanyola del Vallès, Spain.*

[4] *InForest Jru (CTFC-CREAF), Crta. Antiga St Llorenç de Morunys km 2, 25280, Solsona, Catalonia, Spain.*

[5] *CSIC, 08193, Cerdanyola del Vallès, Spain.*

[6] Institut des Sciences de l'Evolution, Université de Montpellier, CNRS, IRD, EPHE

[7] Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, 46 Vanemuise St., 51014 Tartu, Estonia

[8] Estonian Ornithological Society, 4 Veski St, 51005 Tartu, Estonia

[9] Sovon Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, The Netherlands

[10] Department of Animal Ecology & Physiology, Institute for Water and Wetland Research, Radboud University, PO Box 9010, 6500 GL Nijmegen, The Netherlands

[11] European Bird Census Council, P.O.Box 6521 6503 GA Nijmegen, The Netherlands

[12] Department of Bioscience, Aarhus University, Grenaavej 14, 8410 Roende, Denmark.

[13] DOF-BirdLife Denmark, Vesterbrogade 140, DK 1620 Copenhagen V, Denmark.

[14] Catalan Ornithological Institute, Natural History Museum of Barcelona, Plaça Leonardo da Vinci 4–5, 08019, Barcelona, Catalonia, Spain.

[15] Natuurpunt Studie, Coxiestraat 11, 2800 Mechelen, Belgium

[16] Canadian Wildlife Service, Environment and Climate Change Canada, 1125 Colonel By Drive, Ottawa, Canada

[17] UMR7204 Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), MNHN CNRS Sorbonne Université, Paris, France.

[18] Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

[19] Conservation Science Group, Dept of Zoology, University of Cambridge, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK

[20] Lab of Ecologie, Systematique & Evolution,UMR CNRS 8079, University Paris-Sud, France

[21] National Audubon Society, 220 Montgomery St Ste 1000, San Francisco, CA 94104

[22] Birdlife Estonia / Estonian Ornithological Society, Veski 4, Tartu, Estonia

[23] Natagora, Département Études, Traverse des Muses, 1, B-5000 Namur, Belgium

[24] University of Nyíregyháza, Nyíregyháza, Sóstói út 31/b, H-4401, Hungary

[25] MME/BirdLife Hungary, Budapest, Költő utca 21, H-1121, Hungary

Abstract

1. Global climate change is driving species' distributions towards the poles and mountain tops during both non-breeding and breeding seasons, leading to changes in the composition of natural communities. However, the degree of season differences in climate-driven community shifts has not been thoroughly investigated at large spatial scales.

2. We compared the rates of change in the community composition during both winter (non-breeding season) and summer (breeding) and their relation to temperature changes.

3. Based on continental-scale data from Europe and North America, we examined changes in bird community composition using the community temperature index (CTI) approach and compared the changes with observed regional temperature changes during 1980–2016.

4. CTI increased faster in winter than in summer. This seasonal discrepancy is probably because individuals are less site-faithful in winter, and can more readily shift their wintering sites in response to weather in comparison to the breeding season. Regional long-term changes in community composition were positively associated with regional temperature changes during both seasons, but the pattern was only significant during summer due to high annual variability in winter communities. Annual changes in community composition were positively associated with the annual temperature changes during both seasons.

5. Our results were broadly consistent across continents, suggesting some climate-driven restructuring in both European and North American avian communities. Because community composition has changed much faster during the winter than during the breeding season, it is important to increase our knowledge about climate-driven impacts during the less-studied non-breeding season.

Keywords community composition, community ecology, environmental change, global warming, long-term monitoring, population dynamics

Introduction

Global climate change is influencing species' behaviour, distribution, morphology, and population sizes at a range of spatial and temporal scales (Couvet & Jiguet, 2008; De'ath, Lough & Fabricius, 2009; Devictor, Julliard, Parmesan, 2006). For example, climate change is responsible for the shifting distribution and abundance of many species towards poles and mountain tops (Amano et al., 2020; Austin & Rehfisch, 2005; Davey, Devictor, Jonzén, Lindström & Smith, 2013; Devictor et al., 2008; Fossheim et al., 2015; Guerin, Wen, & Lowe, 2012; Lynch et al., 2016; Parmesan, 2006; Sheldon, 2019; Stephens et al., 2016). Furthermore, areas experiencing larger increases in temperature have experienced faster changes in species' breeding distributions (Chen et al., 2011), which in turn influence the composition and biodiversity of regional communities (Davey et al., 2013).

Studies investigating observed changes in animal communities under climate change across multiple continents are rare. Existing publications show that increasing temperatures can affect many populations of species across broad geographic regions. Antao et al. (2019) showed in a multi-taxa study that global warming increased species richness in the temperate zone, especially in oceans. Lenoir et al. (2020) described how species are tracking their climatic niche faster in oceans than on land. Although, climate-driven changes in species communities are also evident on land. In the terrestrial realm, La Sorte et al. (2009) reported increasing species richness in the winter bird community of North America. Stephens et al. (2016) highlighted that long-term population trends of breeding birds have changed in accordance with temperature changes across Europe and North America. In a global assessment, Spooner et al. (2018) found that populations of birds and mammals have declined more in areas with larger temperature increases. Amano et al. (2020) also documented links between temperature increases and global waterbird population declines, with the strongest effects in tropical latitudes where 69% of species declined in response to temperature. Another perspective on climate-driven community changes is from changes in the structure of species communities. For instance Princé & Zuckerberg (2014) found that warm-dwelling species had increased in winter garden bird communities in eastern North America. Furthermore, Devictor et al. (2012a) reported increasing dominance of warm-dwelling breeding birds and butterflies in Western Europe.

The biotic community in a given area changes within a year, as dispersive and migratory species and individuals move in or out of the area. For instance, each fall, Eurasian and North American bird communities are substantially altered as a large number of species migrate to more southern latitudes for the boreal winter (Newton 2008). Impacts of climate change on migratory

species can be different across winter, summer, and migratory seasons. Although most studies of distribution change have been on species' breeding distributions, evidence also suggests that climate-driven shifts in the distribution and abundance of migratory species have occurred in the winter (Amano et al., 2020; La Sorte & Thompson, 2007; Lehikoinen et al., 2013). A comprehensive national case study showed that Finnish winter land bird communities have changed slightly faster than summer communities, although both still lag strongly behind observed temperature changes (Devictor et al., 2008; 2012a; Santangeli & Lehikoinen, 2017).

To improve our understanding of how natural community composition has changed seasonally and spatially, and subsequently the mechanisms underlying these changes, we examined how bird communities have changed in relation to climate change across large spatial scales. We combined large-scale, long-term, multiple-species data on summer and winter bird communities across Europe and North America, and investigated two macro-ecological questions: 1) Are there regional differences in community responses to climate change? We predicted that annual and long-term changes in regional community composition would be explained by annual and long-term regional temperature changes, respectively. We expected that winter communities would be influenced by temperatures of the same winter, through impacting short-term survival and redistribution (Austin & Rehfisch, 2005; Pearce-Higgins, Eglington, Martay & Chamberlain, 2015). In the summer communities we predicted that temperature would have a one year lag effect: summer temperature would influence breeding success, which would affect communities the following year when young are recruited to the population (Lindström et al. 2013, Pearce-Higgins, Eglington, Martay & Chamberlain, 2015). In both cases, we also tested whether the connection between temperature and annual community composition change differs between regions.
2) Are there seasonal differences in community responses to climate change? We expected winter community composition to change faster for a given degree ºC change than summer community composition, because (i) individuals more readily shift their non-breeding areas (Newton, 2008), and (ii) winter temperatures may more strongly constrain bird distributions (Zuckerberg et al., 2011).

To answer these questions, we examined long-term changes in bird communities using monitoring data from 57 regions (states, provinces, or countries) in Europe and North America, in both winter (December-January) and summer (mainly May-June) in 1980–2016 (Tables S1–2).

Material and methods

Data collection

We used data from 10 long-term bird monitoring programs focused on either the summer or winter season. These programs provided data from the United States and Canada in North America, and nine countries in Europe (Table S1). Winter surveys were conducted during December and January; breeding season surveys were conducted from March until early July (mainly during April – June, exact period varied by the latitude and altitude to match regional species' breeding phenology). All bird species were counted in the surveys, but we excluded all non-native species from the analyses, as their distributions are typically more dynamic and variable, in ways not driven by climate (they typically represent <1% of all individuals in each region). We defined the spatial unit of interest (hereafter region) as country in Europe and 5ºx5º grids in North America. We used countries as units in Europe because they often had different survey methods, whereas in North America the winter and breeding schemes are the same in all states and provinces. However, to increase the spatial resolution in Europe, we split both Finland and Sweden into two regions (see Tables S1–2). Altogether, this resulted in 57 regions across the two continents, each of which had at least five locations surveyed annually during both winter and summer. Our analyses included over 1200 species and > 2.8 billion recorded birds (Tables S2–3). We used data from 1980–2016, but shorter time-periods were used in 8 regions (14% of all regions) because monitoring programs in those regions were initiated after 1980 (Table S1). We included these shorter time-periods because our study unit was annual rate of change in the community temperature indices (CTI; see details below and in Devictor et al., 2008; Lindström et al., 2013), and thus data from the shorter time periods were comparable. Furthermore, in North America (but not in Europe) the number of routes (census locations) and the spatial coverage of sampling has clearly expanded since the 1980s and we used only those routes that were established before 1985 to keep the spatial coverage of the sampling similar across time.

The rate of change in the community was measured using CTI. CTI is a metric reflecting the average thermal preferences of all birds (measured as "species temperature index", STI) occurring in a given assemblage (see Data Analysis). The units of both CTI and STI are both ºC and can thus be used to quantify changes (Devictor et al., 2008, 2012a; Lindström, Green, Paulson, Smith & Devictor, 2013; Oliver et al., 2017; Santangeli & Lehikoinen, 2017; Tayleur et al., 2016). If CTI

increases over time, species with warmer niches have become relatively more common than species with colder niches. To calculate annual changes in regional temperature, we used the time periods from the bird data within each region. This ensures that the CTI and temperature data were comparable within regions despite varying time spans (see calculations in the statistical analyses below).

The monitoring sites are not necessarily the same during winter and summer, which can add some additional noise to the data as the same habitats may not be equally sampled during both seasons. To control for these differences, we conducted a separate local comparison using Swedish point count data (Table S1). Here we compared only those sites which were surveyed during both summer and winter during the same years (e.g. winter 1975/76 and summer 1976). These data covered winters 1975/76 – 2015/2016 and summers 1976–2016 and included 389 routes with regular point counts.

Statistical analyses

Within each region (country or grid cell), each sample was a count of all bird species detected along a defined 'route' (Table S1). We calculated annual CTI for each bird monitoring site in each year, based on the counts of each species detected on the surveys and the STI (Devictor et al., 2008). STIs represent the long-term average temperature within the range of the species for a given season (winter or summer). We calculated one winter STI (STI_{wi}) and one summer STI (STI_{su}) for each species per continent. Different STI values were needed for winter and summer seasons, since a given species' temperature niche is likely different between seasons, especially for residents wintering in northern latitudes (Ponti, Arcones, Ferrer & Vieites, 2020). As an example, if in a simple two-species community, species A and B are equally abundant, and have STI values 6 and 10, respectively, the CTI of the community is 8. If species A is twice as abundant as species B the CTI would be 7.3 (2/3 * 6 + 1/3 * 10). In contrast, if species B were twice as abundant as species A, the CTI would be 8.7 (1/3 * 6 + 2/3 * 10). We used abundance instead of presence-absence data, because we were interested in changes in community structure and not only species turn-over rates. For instance, a ten-fold increase or decrease in species abundance can influence a community's structure while not affecting the presence-absence of the species (Lindström et al., 2013). Therefore, a CTI based on abundance is more sensitive to changes than a

CTI based only on species occurrence, which requires local colonisation or extinction to register a change to CTI.

For European species, we used existing STIsu values (Devictor et al., 2012), which were calculated using the breeding ranges from the European Bird Census Council (EBCC) atlas of European breeding birds (Hagemeijer & Blair, 1997). Devictor et al. (2012b) found that STIsu calculated using different distribution datasets showed very high positive correlation ($r = 0.96$), because species occurring in higher or lower latitudes do so in all distribution datasets. Furthermore, long-term changes in CTI did not differ between different species-specific STIsu based on various distributional datasets (Devictor et al., 2012b). Therefore, even though species ranges are likely changing due to climate change, these changes are not yet so dramatic that they might substantially change the climatic niche of the species. For a thorough analysis, see Devictor et al. (2012a,b).

To mirror the European STIsu, we calculated STIsu for North American species following Devictor et al. (2008, 2012b). We calculated the average temperature of the typical breeding months (March–August) for each species' breeding range over the period of ~1950–2000 (obtained from WorldClim.org at a resolution of 30-arc seconds, Fig. S1; Hijmans, Cameron, Parra, Jones & Jarvis, 2005). We used the breeding ranges provided by Birdlife International and the Handbook of the Birds of the World (2017). The STIsu values were used to calculate CTI within North America, so we restricted the area for calculating the STIsu to North America (including Canada, the United States, Mexico, and Greenland) despite the fact that some species may also have populations outside these regions. The selection of months likely has a low impact on the relative STI. For example, the STIsu in North America calculated using March–August months are highly correlated with the STIsu based on April–July months ($r_p = 0.999$; Fig. S2).

We calculated the European STIwi in previous work (method explained in Santangeli & Lehikoinen 2017). We used the same procedure and data sources to calculate the North American STIwi. More specifically, for each species' wintering range in each continent, we calculated the average temperature of the winter months (December, January and February) over the period of ~1950–2000 (obtained from WorldClim.org at a resolution of 30-arc seconds) (Hijmans et al., 2005). We selected all birds that regularly overwinter in North America (i.e., the Greenland, Canada, United States, and Mexico) using the distribution ranges provided by Birdlife International and the Handbook of the Birds of the World (2017). We selected the part of the distribution where the species is either resident or non-breeding. To calculate the STIwi we used

distributions from both North and South America (Fig. S1), as many of the study populations spend their winter months in South America. Similarly, we included wintering areas of European breeding birds which in Africa and Asia when calculating STIwi (Santangeli & Lehikoinen 2017). It is important to note that STI is not an absolute measure of the species climatic niche as it does not distinguish the breadth of the niche. Rather, STI should be considered as a relative measure ("index") of a species' climatic affinity (for a thorough discussion of STI, see Devictor et al., 2012a,b). All STIs are provided in Table S3.

All spatial analyses were conducted with ArcMap 10.1 (ESRI, Redlands, CA). To evaluate whether species that occur in colder conditions during the breeding season also occur in colder conditions during the winter season, we used the Pearson correlation to test whether the summer and winter STIs of species were correlated.

The annual route-specific CTIs were computed using the STIs and counts of species on each route in each year. Then we modelled region-specific CTIs for winter and summer using linear mixed effect models with a Gaussian distribution, where each route-specific CTI was the response variable, explained by year (as factor variable) and route (as a random factor) (Devictor et al., 2008; Tayleur et al. 2016). Furthermore, we used the same model structure to measure the long-term trend in CTI, except that year was used as a continuous variable (Devictor et al., 2008; Tayleur et al. 2016). Both the annual regional CTI and the long-term changes in regional CTI were used as response variables in the final analyses. These measures were also calculated separately for Swedish point count data, where the same sites had been surveyed in both summer and winter in each year. The analyses were conducted in R (version 3.6.2; R Core Team, 2019; see the details of the packages used at the end of the methods).

To measure regional temperature changes, we used the observed monthly temperature anomalies in 5°x5° grids data from Earth System Research Laboratory (Jones et al., 2012), which were the same grids as used in the North American CTI analyses. We calculated temperature changes for each region for winter months (December and January, prior to and during the census periods) and summer months (April through July, which are known to influence species' breeding success) (Newton, 2008; Grimm et al., 2015; Meller, Piha, Vähätalo & Lehikoinen, 2018). We used linear regression to calculate the rate of change in the seasonal temperatures for each region using the same study years as the bird data for each region. Furthermore, to measure the spatial differences in climate, we used monthly mean temperatures (December – February for winter, March – August for summer) of the same WorldClim data for 1950–2000 that were used to

calculate the STI. The rationale for this variable was to derive a temperature gradient between regions, i.e. to test how well the regional mean CTIs match with the observed mean temperature values from the areas during the same period 1980–2016, to determine the slope between these variables, and distinguish any seasonal differences (Fig. 1). The slopes were calculated using Gaussian linear regression and *a priori* we did not expect differences between continents in the relationships.

In the final analyses, we first examined whether annual regional CTI values were explained by the CTI of the previous year (continuous variable, standardised regionally to account for temporal autocorrelation), annual regional changes in temperature within a particular season (continuous variable), and continent (factor variable, Europe or North America). We ran the analyses separately for the winter and summer seasons. For the summer season, annual temperature change was calculated between years t-1 and t-2 as summer weather during the preceding year may influence breeding numbers through reproduction and recruitment (e.g., high temperatures lead to increased breeding success, which causes population increases during the following year) (Meller et al., 2018; Pearce-Higgins et al., 2015). For the winter season, temperature change was calculated between year t and t-1, as winter weather can influence spatial variation in species abundance within the same winter season due to climate-driven movements or mortality of individuals (Austin & Rehfisch, 2005; Newton, 2008; Pearce-Higgins et al., 2015). Region was a random factor in both summer and winter analyses, and therefore we compared two model combinations, with and without random slope of temperature, to see if a potential impact of temperature was region dependent. The models were ranked based on AICc (Burnham & Anderson, 2004).

Furthermore to test for continental differences in responses, we used linear mixed models to model relationships between long-term changes in CTI and season (factor variable, summer or winter), rate of change in temperature (continuous variable) and continent (factor variable, Europe or North America). As in the analyses of between-year variation described above, we included interactions between: i) temperature change and season, and ii) continent and season, to investigate potential continental and seasonal differences. To take account of the uncertainty in CTI trends, we weighted the observations in the analyses with the reciprocal of the variance of the trends as estimated by the previous analysis. In the long-term analyses, region was used as a random factor. There was no strong collinearity between variables used in the models (all $|r| < 0.5$) (Booth, Niccolucci & Schuster, 1994). Altogether, our long-term analyses included six model

combinations (Table S4), and we ranked them by the resulting AICc (Burnham & Anderson, 2004).

Finally, we compared observed and predicted regional rates of change in CTI with a linear model. The predicted changes in CTI were based on observed temperature changes in each region during 1980–2016 (shorter time periods in some regions; see Table S1) and the slope between regional mean temperatures and CTIs (see Fig. 1). The response variable was observed or predicted CTI change and the explanatory variables were data type (observed or predicted), continent and their interaction. The analyses were conducted separately for the summer and winter seasons and we used the above mentioned weighting in the long-term analyses.

For the linear mixed effect models, we used the functions lmer (package lme4; Bates, Maechler, Bolker & Walker, 2015) and lmerTest (package lmerTest; Kuznetsova, Brockhoff & Christensen, 2017) unless there was singularity problem. In such cases we used blmer (package blme; Chung et al., 2013) for both the annual and the long-term analyses function in R (R Core Team, 2019). For Pearson correlation and linear regression we used function cor.test and lm in R.

Results

The STIsu and STIwi were positively correlated in both Europe ($r_p = 0.299$, df $= 302$, $P < 0.001$) and North America ($r_p = 0.485$, df $= 561$, $P < 0.001$; Fig. S3, Table S3).

As expected, there was a strong positive association across regions between mean atmospheric temperature and average CTI during 1980–2016 (Fig. 1A–B). However, the slope between mean CTI and mean temperature differed between seasons and was slightly, but significantly, steeper during winter (LMM, interaction, t $= 4.34$, n $= 113$, $P < 0.001$, with region within continent as a random factor; Fig. 1A–B). Thus, one Celsius degree difference in mean temperature between two regions was associated with a larger regional difference in CTI during winter than in summer (Fig. 1A–B). Therefore, we could expect that the same magnitude of temperature increase would produce a larger change in CTI in winter than in summer.

Over time, we observed that European bird communities have become increasingly dominated by warm-dwelling species during both winter and summer. Long-term average annual rates of change

in CTIwi and CTIsu were estimated at +0.025 ± 0.006 SE and +0.004 ± 0.001 SE, respectively (Fig. 2). This pattern was similar in North America during the winter; long-term average annual rate of change in CTIwi: +0.032 ± 0.002 SE, but CTIsu in North America did not change significantly (+0.002 ± 0.002 SE), although the slope was positive (Fig. 2).

Both CTIwi and CTIsu increased in the Swedish point count routes, where the same routes and years were used, but CTI increased over seven times faster during winter (+0.038 ± 0.004 SE, t = 9.31, n = 3362, P < 0.001) than during summer (+0.005 ± 0.001 SE, t = 8.03, n = 3362, P < 0.001). The annual variation was also much larger during winter than summer (Fig. S4).

During both winter and summer, the models including random slope for annual temperature effect had much smaller AICc values than the model without the random slope (winter ΔAICc = 40.7, summer ΔAICc = 4.65). This suggests that increases in temperature has different effects in different places. According to the top ranked models, the annual changes in CTI were significantly positively correlated with annual changes in temperature during winter and summer, but the slope of the winter relationship was notably steeper (Fig. 3A–B, Tables S4–5).

Overall, long-term (i.e. 1980–2016) changes in CTI were positively associated with the long-term temperature changes in the 57 regions (P = 0.051; Table S7). The rate of long-term change with temperature change was numerically similar across continents and seasons, although the relationship between CTI and temperature change was not statistically significant during winter due to higher uncertainty (Figs 3C–D, linear regression: winter β = +0.123 ± 0.096 SE, P = 0.21, summer β = +0.122 ± 0.046 SE, P = 0.0097). In addition, long-term changes in CTI were significantly greater in winter than in summer (Figs 2A–D, Tables S7).

In the analyses comparing the observed and expected CTI changes, the significant interaction between data type (observed or expected) and continent suggested that observed CTI changes in winter were larger than expected in North America but not in Europe (Table S8; Fig. 2C) (average slopes of the areas: North America: CTI change 0.027 ± 0.002 SE and expected CTI change 0.019 ± 0.001 SE ºC/year, Europe: CTI change 0.025 ± 0.005 SE and expected CTI change 0.035 ± 0.009 SE ºC/year). However, in summer, communities strongly lagged behind the expectations based on the observed temperature change, and similarly so in both continents (average of the areas: North America: CTI change 0.002 ± 0.001 SE and expected CTI change 0.090 ± 0.001 SE ºC/year, Europe: CTI change 0.003 ± 0.001 SE and expected CTI change 0.005 ± 0.004 SE ºC/year; Fig. 2D). This suggests that winter communities have changed faster and have followed temperature changes more closely than summer communities.

Discussion

We found that both temperature and CTI increased in most regions during both winter and summer, but the changes were much faster during winter. As expected, we found a positive relationship between the speed of community composition changes and temperature changes, during both annual and long-term analyses (the latter only during summer), which supports our first prediction. This suggests that the observed changes in community composition are at least partly driven by changes in temperature, but we cannot exclude that other environmental factors may have also contributed to the observed changes in community composition (Clavero et al., 2011). Our results showed that there were regional differences in how strongly avian communities have responded to annual temperature changes.

Various factors may explain why the regional speed in long-term changes in community composition did not always follow the regional long-term rate of changes in temperature. First, several earlier studies have shown that bird and butterfly communities did not respond as fast as expected based on observed temperature change (Devictor et al., 2008; 2012a), thus time lags in responses are expected and such lag effects may vary regionally. However, in our case the winter CTI change in North America changed even faster than expected based on temperature change. Second, the compositions of the communities vary regionally and therefore different species contributed to the regional CTI changes. Several studies have also shown that species are not responding equally to climate change and speed of range shifts vary among species (Pöyry et al., 2009; Davey et al., 2013; Lenoir et al., 2020). Third, a weak connection between the long-term trends of CTI and temperature can also be affected by temperature changes outside the particular sampling location. Temperature changes in different regions may affect winter movement of individuals to particular locations and thus influence the community structure (e.g. Sauter, Korner-Nievergelt & Jenni, 2010). Last, other anthropogenic factors such as land use change or winter feeding (Prince & Zuckerberg, 2014; Howard et al., 2020), can affect regional community structure and thus influence changes in CTI. For instance, winter feeding may increase the survival of southern species as they expand into northern regions and thus lead to increased dominance of these species (Princé & Zuckerberg, 2014, Fraixedas et al., 2015). Winter feeding is therefore a potential driver of winter CTIs increasing faster than predicted by temperature, especially in North America.

We must also stress that potential regional changes in the monitoring sites might influence local changes in the CTI even though the site id was included as a random factor. We do believe, however, that this is adding random noise into data rather than adding bias to the results in a particular direction.

We did not find a significant positive long-term trend in the North American summer CTI, in contrast to the European CTI. This contradicts the results in Stephens et al. (2016), where warm-dwelling species were clearly increasing their populations in North America compared to cold-dwelling species. However, the set of species and the spatial structure of the analyses are different between these studies, which may explain the different findings. Our analyses also include species too rare to calculate species-specific annual trends and we also analyse data in smaller spatial units. In addition, we note that the slope of the North American summer CTI was positive although not significant due to high variation between regions.

As we predicted, winter communities responded more closely to annual temperature changes than summer communities, and winter communities also changed faster than summer communities. We suggest two likely explanations for these seasonal differences: demographic effects of winter temperature are more direct, and individuals are less site-faithful in winter and can therefore respond more readily to changes in weather.

First, winter populations are more likely to be directly affected by temperature-driven mortality, due to physiological limitations; cold temperatures can thus limit species distributions in winter (Zuckerberg et al., 2011). Conversely, changes in breeding communities take place through more complex demographic processes, including variation in reproduction and recruitment of young to the population and philopatry of breeders (Lindström et al., 2013, Pearce-Higgins et al., 2015). This may lead to delayed and diluted effects of climatic conditions, which could be the reason why we did not detect an effect of temperature on breeding communities at the annual level (one year lag). In line with this, in an analysis of four Swedish datasets, Lindström et al. (2013) found evidence of two and three year lags between summer temperature and CTI. The strong annual variation of the winter CTI compared to summer CTI in (also apparent in the Swedish point counts analyses, Fig. S4) demonstrates the clear differences in community dynamics between seasons.

Second, winter communities are more likely influenced by movements of individuals from one place to another (Austin & Refisch, 2005; Lehikoinen et al., 2013; Golet, Jaffre, & Devictor, 2011). Individuals are more likely to show stronger philopatry to their breeding areas than their

wintering areas (Batt, 1992, Guillemain et al., 2013), which enables winter communities to be more mobile. For instance, songbirds wintering in our boreal and temperate study areas tend to have low site-fidelity (Sandercock & Jaramillo, 2002). Both of these factors could help explain why winter communities show larger between-year variation than summer communities (see e.g. Fig. S3).

Many climate change studies on animal communities have concentrated only on their breeding season (Santangeli & Lehikoinen, 2017), whereas our study provides evidence that wildlife responses are seasonally and spatially variable, and can be much stronger during the non-breeding season. Since processes during the non-breeding season can affect the subsequent breeding season through survival and preparation for reproduction (i.e., carry-over effects; Birkhead et al., 1983, Pearce-Higgins et al., 2015; Norris, Marra, Kyser, Sherry & Ratcliffe, 2004; Sandeman, Yaragina & Marshall, 2008, Saether et al., 2010), it is important to expand our understanding of effects of climate-driven impacts into the non-breeding season. Our findings also highlight that there is a positive connection between winter and summer STI values of species that reflect the climatic preference of species. This indicates that warm-dwelling species tend to also occur in warmer areas also during the winter season. However, there is a strong variation among species and therefore a relatively weak overall correlation (Fig. S3, Ponti et al. 2020).

Overall, our results show that a warming climate can trigger rapid reshuffling of avian communities across large spatial scales, with winter communities responding more quickly to changes in temperature than summer communities, even faster than expected based on observed temperature changes. The latter also highlights that strategies to protect species of conservation concern will need to be flexible and dynamic enough to cope with rapid change, particularly those occurring on the non-breeding grounds (Pavón-Jordan et al., 2015), which historically have received less conservation attention than those on the breeding grounds. Future research should aim to identify species that are driving the changes and to understand which other factors contribute to spatial variation in community change or provide resilience to climate change, such as habitat change, winter feeding, hunting or recovery from persecution and pesticides (Newton, 1998; Zuckerberg et al., 2011). Changes in CTI can be caused by an increase in warm-dwelling species, a decrease of cold-dwelling species or a combination of both, so subsequent analyses are needed to identify the species driving the changes (Davey et al., 2013; Lindström et al., 2013; Tayleur et al., 2016). Determining the drivers of temperature-related changes in bird community composition will help conserve bird populations during escalating global climate change.

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Data availability

The data and the R codes to replicate the study are available in Dryad (Lehikoinen et al. 2021).

Fig. 1. Connection between mean community temperature indices (CTI) and mean seasonal temperatures during 1980–2016. The positive relationship between regional, long-term mean community temperature indices and long-term mean temperatures in Europe (black dots) and North America (open dots) during a) winter (slope = 0.549 ± 0.024) and b) summer (slope = 0.426 ± 0.014). Each point represents a single region. All the variables are centred at zero. The line shows the estimated relationship and the grey area indicates the 95% confidence intervals.

Fig. 2. Long-term changes (ºC / year) in regional community temperature indices, CTI. Spatial distribution of CTI changes (a–b), and regional observed and expected CTI changes based on temperature changes (c–d) in Europe (11 regions) and North America (46 regions) during winter (a and c) and summer (b and d) season. The box plots show observed changes in CTI compared to expected changes based on observed temperature changes in each region during 1980–2016 and the relationship between mean CTI and temperature (see Fig. 1). The box represents the central 50% of the observations and the line within the box indicates the median of the observations. Whiskers represent the rest of the observations and dots are outliers. The grey lines show the zero change level.

Fig. 3. The relationship between change in CTI and change in temperature. Regional between-year changes in European and North America CTI in relation to between-year temperature changes in a) winter (between year t and t-1; one dot is one year in one region; b = +0.052 ± 0.007 SE, P < 0.001; Table S4) and b) summer (between year t-1 and t-2; one dot is one year in one region; b = +0.002 ± 0.001 SE, P = 0.04; Table S5). Regional long-term changes in CTI in relation to corresponding long-term changes in temperatures during c) winter (b = 0.123 ± 0.096, P = 0.207) and d) summer (one dot is one region) (b = 0.122 ± 0.046, P = 0.010). X-axis values in panels a–b are the yearly temperature differences from the mean of each region. In all graphs, the size of the dot indicates the weight of the observation based on uncertainty in the CTI estimates (see methods). The largest dots have the largest weights and the corresponding smallest uncertainty.

(a) Winter

CTI change

● +0.06
● +0.04
· +0.02
· −0.02

(b) Summer

CTI change
● +0.06
● +0.04
• +0.02
• −0.02