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Extreme winter weather disrupts bird occurrence and abundance patterns at geographic scales

Jeremy M. Cohen, Daniel Fink and Benjamin Zuckerberg

J. M. Cohen (https://orcid.org/0000-0001-9611-9150) ✉ (jeremy3cohen@gmail.com) and B. Zuckerberg, Dept of Forest and Wildlife Ecology, Univ. of Wisconsin–Madison, Madison, WI, USA. – JMC and D. Fink, Cornell Lab of Ornithology, Ithaca, NY, USA.

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Extreme weather events are increasing in frequency and intensity as a result of modern climate change. During winter, species may be especially vulnerable to extreme weather as they are surviving on scarce resources and living at the edge of their thermal limits. We compiled data from eBird, a global citizen science initiative, to examine how 41 eastern North American birds shifted their occurrence and abundance patterns immediately following two recent extreme weather events each affecting > 2 million km^2, the intrusion of a polar vortex and a winter heat wave. eBird data is continuously collected at high spatiotemporal resolution across large spatial extents, allowing us to compare species' responses immediately before and after these extreme events with trends in other winters across geographic scales. Overall, we found that birds responded differently to each extreme weather event. Bird occurrence rates did not change following the polar vortex, but where species occurred, population density was temporarily reduced, suggesting reductions in number of individuals driven by decreases in behavioral activity or temporary movement out of the area. However, birds demonstrated widespread increases in occurrence and increases in density and number of individuals where they occurred for at least 20 days after the heat wave, hinting at longer-term range changes. Smaller-bodied, warm-adapted passerines tended to be most sensitive to extreme weather and responded most negatively to the polar vortex and most positively to the heat wave, while larger-bodied, cold-adapted waterbirds expressed only mild responses to either event. Thus, certain species may be exceptionally sensitive to extreme weather events while others are less sensitive. As climate change progresses and climatic variability increases, researchers and managers must better quantify the broad-scale sensitivity of different species to multiple types of extreme weather events.

Keywords: climate change, climate change ecology, eBird, extreme weather, macroecology, species distribution models

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Introduction

Increasing variability in temperature and precipitation over recent decades is resulting in the proliferation and intensification of extreme weather events (Wallace et al. 2014, Cohen et al. 2018). Although extreme weather events are increasing in frequency throughout the year (Rahmstorf and Coumou 2011), extreme weather during winter may leave wildlife exceptionally vulnerable as many species are already living at the razor's edge – operating with scarce food resources and temperatures often at the lower end of their thermal limits (Salewski et al. 2013, Penczykowski et al. 2017, Casson et al. 2019). Several types of winter weather events have the potential to impact northerly ecosystems and their dependent species – disrupting behavior, distributions and survival – despite lasting only days (Martin 2017, Birgander et al. 2018, Kreyling et al. 2019, Latimer and Zuckerberg 2019). For instance, the intrusion of the polar vortex into central and eastern North America during winter has become more common and intense as arctic warming has destabilized the jet stream separating arctic and temperate air masses, resulting in extremely cold air outbreaks in temperate areas sustained over several days to a week (Cohen et al. 2014). Furthermore, unseasonably warm periods have increased in both frequency and duration, sometimes resulting in early summer temperatures during winter (Di Lorenzo and Mantua 2016, Yu et al. 2019). However, few studies have examined how species respond in the days or weeks following extreme winter weather events at regional and continental scales because high-volume, continuous observations before, during and after such events are scarcely available at high spatiotemporal resolution, especially for multiple species or across large spatial extents. Further, few studies have examined how extreme weather impacts multiple aspects of population status, such as occurrence and abundance. Thus, it remains unclear how extreme winter weather events impact wildlife, whether these impacts are typically short-lived or long-lasting, and which species are most likely to be vulnerable.

Species may exhibit distinct responses to extreme weather events, including changes in behavioral activity, die-offs or increased movement (Salewski et al. 2013, Penczykowski et al. 2017, Casson et al. 2019). Such responses could manifest as changes in occurrence and abundance that persist across different periods of time, highlighting the importance of examining species' responses to extreme weather at high temporal resolution. For example, an extreme weather event may induce changes in occurrence (e.g. range contraction) and, in areas where the species occurs, it may also induce changes in population density (e.g. via flocking or spreading out) that last throughout a season or even over years (Clark and Dukas 2000, Moreno et al. 2015). Alternatively, species that shift their behavior (e.g. changes in foraging) may quickly revert to previous occurrence or abundance levels following an extreme event in a matter of days or weeks. As predicted by the abundance–occupancy relationship (Gaston et al. 1999, Zuckerberg et al. 2009), concurrent changes in occupancy and abundance across species should be similar, but specific responses may result in a decoupling of these relationships (Gaston et al. 1999). For instance, flocking, a common response of birds to cold weather (Klein 1988), may result in rapid increases in local abundance with little change in overall occurrence. Alternatively, if extreme weather results in high rates of community turnover, in which individuals spread out to explore new areas, acquire thinning resources or seek out refugia, occurrence may increase while abundance decreases (Borregaard and Rahbek 2010, Latimer and Zuckerberg 2020). Across species, extreme weather events may impact species differently depending on their thermal tolerance or functional traits. For instance, a southerly-distributed species with low cold tolerance may be relatively more sensitive than a northerly species to an extreme weather event in which temperatures plummet (Sauer et al. 1996, Latimer and Zuckerberg 2020), whereas small-bodied species may be most sensitive to an extreme weather event because they have low thermal inertia (Huey et al. 2012, Albright et al. 2017).

Currently, little is known about how species respond to extreme weather events in winter (but see Casson et al. 2019, Latimer and Zuckerberg 2019), as this assessment necessitates high volumes of continuously recorded data on species' occurrences and counts at high spatiotemporal resolution. Birds are an excellent model taxa as they are easily detectable, are widely considered indicators of environmental change, and expend energy at high rates, making them sensitive to fluctuations in weather (Knudsen et al. 2011) across temporal scales (Cohen et al. 2020). Herein, we examined bird responses to extreme winter weather events using occurrence and count data from eBird, a global citizen science initiative in which users contribute checklists of birds observed at a specific location, date and time (Sullivan et al. 2014). Citizen science data has become widely recognized as a valuable resource enabling the analysis of species distributions over broad geographic extents at fine spatiotemporal resolution (Zuckerberg et al. 2016). eBird has over 650 million contributed records collected in a continuous fashion (La Sorte et al. 2018), ensuring a high volume of high-resolution data before, during and after extreme weather events, and, importantly, eBird data are collected with ancillary information to correct for biases inherent in citizen science datasets (Kelling et al. 2019).

eBird data has been collected across multiple years in which extreme winter weather events have occurred by chance. Thus, eBird data can be used to assess the biological impact of extreme weather events as a natural experiment; analogous to a before–after impact study (e.g. pre- versus post-treatment changes; De Palma et al. 2018) in which species' occurrence and counts are compared before and after an event and during the same time period in other years. Our goal was to examine how birds responded to two recent extreme weather events that may expose birds to conditions well outside their typical thermal limitations – the intrusion of a polar vortex (hereafter referenced as 'polar vortex') and a winter heat wave – that each affected about 2 million km^2 of central and eastern North America. Although temperatures during a winter heat wave are well within species' thermal limitations most of the year, many winter-adapted species undergo physiological changes (e.g. seasonal adjustments to summit metabolic rate) to acclimate to cold weather (Liknes and Swanson 2011, Laplante et al. 2019, Jimenez et al. 2020) and may thus be less tolerant of unusually warm weather during the winter months. We had several objectives: 1) compare concurrent changes in occurrence and abundance following each event that may indicate whether the responses are driven by behavioral changes, demography (e.g. die-offs) or distributional changes; 2) assess the duration of species responses to each weather event; and 3) assess whether species responses to events were predictable based on functional traits, such as geographic range, body size, habitat generalism, primary diet and habitat preference. To address issues with abundance modeling of citizen science data (Johnston et al. 2015), we estimated abundance based on checklists where the species already occurs (Methods); thus, our abundance estimates (hereafter, 'conditional abundance') are an indicator of population density or aggregation/disaggregation.

We predicted that both extreme events – a polar vortex and heat wave – would reduce the occurrence and conditional abundance rates of most species, as each event brought a sharp departure from the typical winter conditions. However, we did not have an a priori expectation about whether changes in occurrence and conditional abundance following each event would be similar in magnitude. We predicted that at the same location in space, 'warm-adapted' species or those typically distributed throughout warmer climates, would be more sensitive than 'cold-adapted' species to a polar vortex but least sensitive following a heat wave, and that species that typically experience less climate variability would respond more negatively than others to either event. Further, we predicted to observe higher sensitivity to extreme weather events for 1) small-bodied species that have lower thermal inertia (Huey et al. 2012, Albright et al. 2017); 2) habitat specialists, as thermal and habitat niche breadths are often positively related across species (Barnagaud et al. 2012); and 3) species occupying open areas, such as grasslands or open water, that support fewer microclimatic refugia than forest-adapted species (Jarzyna et al. 2016).

We quantified before–after changes in both occurrence and conditional abundance rates across a suite of widespread eastern North American bird species following the most intense polar vortex and winter heat wave of the previous decade. The polar vortex occurred in January 2014, bringing temperature anomalies of −10°C to about 1.8 million km^2 of the midwest and northeast USA over a four-day period (Fig. 1a; Cohen et al. 2014). The winter heat wave took place in late December 2015 and carried temperature anomalies as high as +15°C across 2.0 million km^2 of the eastern USA for about a week (Fig. 1b; Zhang and Villarini 2017). For common wintering birds in the affected areas (polar vortex: 35 species; heat wave: 41), we used machine learning approaches to predict occurrence and conditional abundance from 10 days prior to the event until 30 days after in the areas that were most affected. Utilizing the occurrence of these extreme events as a natural experiment, we further compared the before–after shifts in bird occurrence and conditional abundance to those over identical time periods in 14 other recent winters to control for typical seasonal trends. Finally, we used multivariate models and model selection to assess how species-level traits were associated with responses to weather events across multiple species.

Methods

Extreme weather events

We examined bird responses to two winter extreme weather events, the 2014 Polar Vortex and 2015 Winter Heat Wave, that each impacted large parts of eastern North America for several days (Fig. 1). These events carried the most extreme, sustained negative and positive wintertime temperature anomalies, respectively, from 2004 to 2018, the period in which sufficient eBird data is available. We defined the period of the polar vortex and heat wave as continuous dates in which the majority of 0.01° cells covering land in northern-temperate eastern North America (designated as a box with dimensions 25°–50°N and 60°–100°W) experienced < -10°C and $>$ +10°C mean temperature anomalies, respectively (regions with points in Fig. 1). Thus, we considered the polar vortex to have covered 4–7th January 2014 (4 days) and the heat wave to have covered 22nd–27th December (6 days), 2015 and hereafter refer to these as 'event dates'. When examining responses to each event, we analyzed checklists from any areas within this region that experienced these temperature anomalies on average over the event dates. Restricting the geographic extent of the analysis in this way has the benefit of increasing power to detect changes in species occurrence and abundance in these regions, however, it limits the ability to directly study shifts in species ranges, which extend beyond these regions for many species.

Daily minimum (for polar vortex) or maximum (for heat wave) temperature anomalies were derived from Daymet, a high-resolution, interpolated grid-based product from NASA that offers daily, 1-km^2 scale weather data across North America (Thornton et al. 2017). Anomalies were calculated by extracting daily baseline values of each weather variable between 1980 and 2003 (the period during which Daymet data are available that is prior any eBird data used in our analysis) for every checklist and subtracting these from the respective values on event dates.

eBird data

We collected all 'complete checklists' (indicating that all detected and identified species were recorded) contributed to eBird in eastern North America (as defined above) between 2004 and 2018, applying a number of filters to the data in accordance with established best practices outlined in Johnston et al. (2019). We limited checklists to those recorded after 2004, the first year exceeding an average of 10 000 user contributions per month in our study area. We also limited

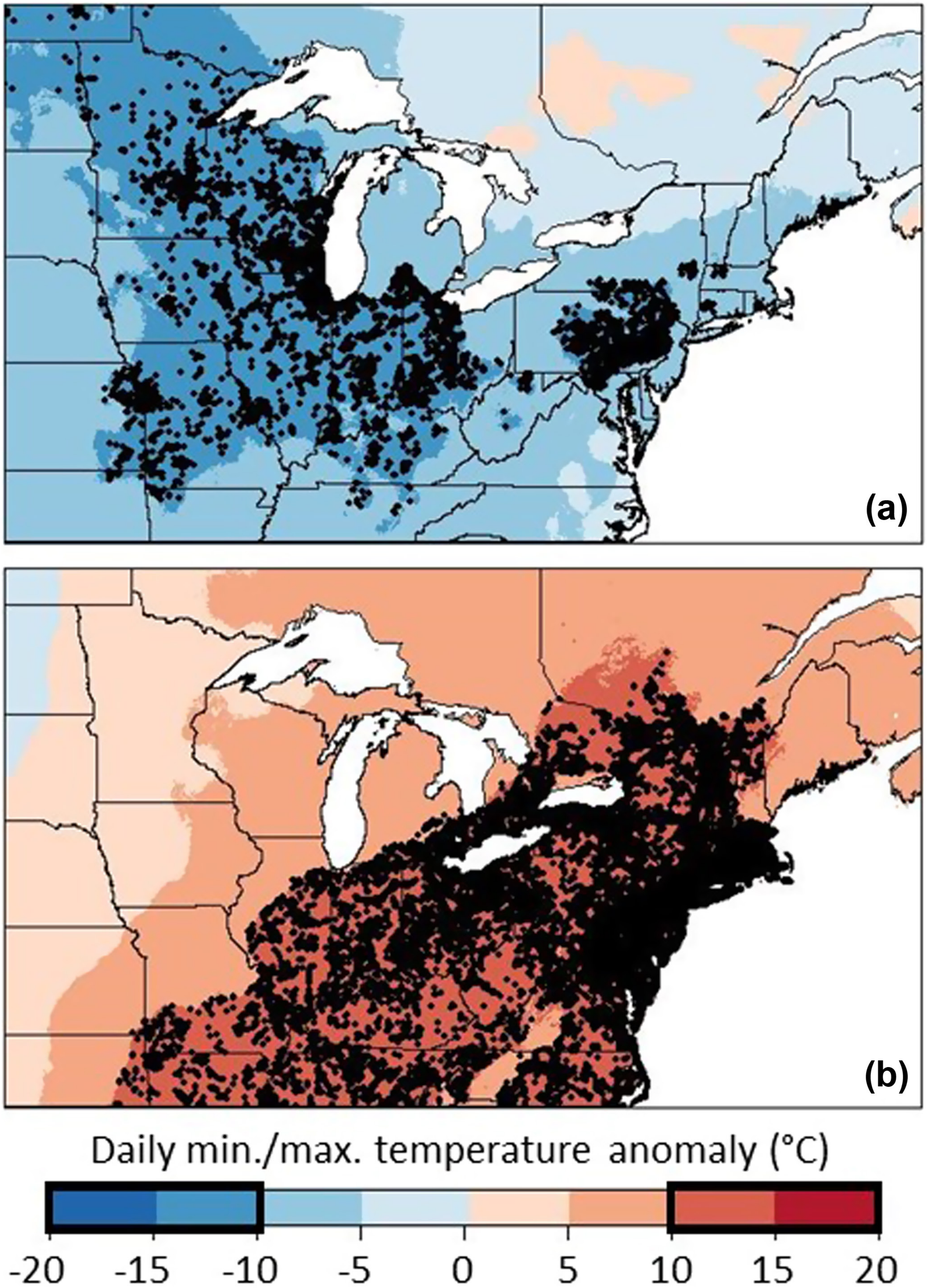

Figure 1. The 2014 polar vortex and 2015 winter heat wave. We examined avian responses to two North American extreme weather events in winter by selecting eBird checklists (points) contributed within greatly affected areas (those with daily mean temperature anomalies of < −10°C for the polar vortex, (a) and > +10°C for the heat wave, (b); denoted by boxes in legend) from 10 days before the events until 30 days after.

checklists to 'traveling' or 'stationary' observations, excluding exhaustive area-counts, which are less numerous and not directly comparable. In all checklists, subspecies information was discarded and observations were summarized at the species level. We excluded checklists with extreme high values of effort (> 3 h or > 5 km traveled) or extreme checklist calibration index (CCI, an index designed to capture inter-observer variation among eBird checklists (Johnston et al. 2018)) scores (z-score < −4 or > 4), which are infrequent and not directly comparable with the bulk of eBird's data.

Our goal was to model occurrence and conditional abundance trends over time in areas impacted by extreme weather events. Therefore, we spatiotemporally filtered the eBird dataset to contain checklists exclusively within the regions significantly impacted by the event (defined above) and on dates shortly before, during and shortly after the event dates (all data compilation and subsequent analyses were conducted in R 3.5.1; <www.r-project.org>). For each event, we first compiled all checklists beginning 10 days before the event and ending 30 days after the event. Second, we included all checklists within the event regions defined above (Fig. 1) and refer to the resulting datasets as the 'event' datasets. Finally, to compare species' changes in occurrence and conditional abundance between event and non-event years, and account for any typical species-level seasonal trends, we compiled all checklists recorded in each of the event areas/regions during the same calendar dates in all other winters between 2004 and 2018 (hereafter referred to as the 'non-event' datasets). To mitigate site selection bias within event and non-event datasets, we also filtered eBird checklists by randomly selecting one observation per 5 km^2 grid cell during each calendar week (Johnston et al. 2019).

Although there are inaccuracies among the point-based locations reported by eBird participants, we do not consider this to be a major concern for this analysis. First, by excluding checklists with distances > 5 km, we eliminated the largest potential locational inaccuracies. Recent analyses comparing the locations reported by eBird participants and the centroid of the GPS locations reported by the eBird app found that on average 86% of all eBird search effort was within a 1.5 km radius of the reported location among searches with total distances of 5 km or less (Auer pers. comm.). Thus, the vast majority of eBird search effort is within a relatively small neighborhood whose size is similar to the spatial resolution of our other predictors, including weather, land cover and topography (below).

Model covariates

We included a variety of covariates in each model to account for the myriad factors that influence species' detection, distribution and recorded counts. First, to facilitate the study of the seasonal progression in species occurrence and conditional abundance before and after each event, we created an 'event date' predictor, defined as the date centered on the weather event, with negative dates before the event, all event dates classified as day 0, and positive dates following the event. Second, to account for variation in detection rates associated with search effort, as well as varying activity levels among birds at different times of the day and among observers, we included time spent birding, number of birders, whether a checklist was categorized as traveling or stationary, distance traveled and CCI as predictors in species distribution models (SDMs, below) following established best practices for modeling eBird data (Johnston et al. 2019). Finally, to account for variation in detection rates associated with weather conditions while birding, we included the mean temperature and total precipitation on the day the checklist was recorded. Third, we gathered land and water cover and topographic data corresponding to each checklist to account for species preferences in landscape composition and configuration. We obtained annual landcover data from the moderate resolution imaging spectroradiometer (MODIS) land cover type (MCD12Q1) dataset, ver. 6 (<https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12q1>). For each checklist, we calculated the proportion and variation of land and water classes within a neighborhood with 1.4 km radius occupied by a variety of landcover types (Hansen et al. 2000), including grasslands, croplands, mixed forests, woody savannahs, urban/built, barren, evergreen broadleaf, evergreen needle, deciduous broadleaf, deciduous needle, closed shrubland, open shrubland, herbaceous wetlands and open savannah. Land-cover data varied annually, although we used 2017 land-cover values for checklists recorded in 2018. We also collected topographical information (median aggregations of elevation, eastness, northness, roughness and topographic position index or TPI at a 1 km^2 resolution) from the Global Multi-Terrain Elevation Dataset, a product of the U.S. Geological Survey and the National Geospatial-Intelligence Agency (GMTED2010; Danielson and Gesch 2011).

Species distribution models: random forest

We modeled responses to extreme weather events in all species with a minimum detection rate of 5% on checklists within the area of each event to avoid low-detection issues. For the 2014 PV and 2015 WHW, this resulted in 35 and 41 species included in our analysis, respectively (Supporting information for list of species).

For each species, we individually fit a two-step hurdle model based on random forests (RFs; Johnston et al. 2015) designed to generate accurate predictions of each species' occurrence rate and median abundance while dealing with the inherent challenges of abundance estimation based on citizen science data, including a high proportion of zero values (Fink et al. 2020). In the first step of the hurdle model, species occurrence is modeled as a binary response with all checklists. In the second step, reported counts are modeled based on the subset of checklists for which the species occurred and for which species was predicted to occur. Thus, our estimates of abundance are conditional on species' occurrence, making them a good indicator of population density or aggregation/disaggregation. For both steps, we use RFs (ranger package; Wright and Ziegler 2015), a flexible machine learning method designed to analyze large datasets with many predictor variables, adjust automatically to complex, nonlinear relationships and consider high-order interactions between all predictors. RFs have been used in a number of species distribution modeling problems (Mi et al. 2017) and have been used to study seasonal variation in the occurrence rates of tree swallows *Tachycineta bicolor* associated with warm winters (Coleman et al. 2020). To predict species' binary state (occurrence/non-occurrence) from the occurrence rate, we estimated the threshold that maximized Cohen's Kappa statistic (Cohen 1960) using out-of-bag training samples. Predictor sets for occurrence and abundance models included all predictors discussed above. The count/abundance model also included the predicted occurrence rate as an additional predictor to allow for proportionate changes between species occurrence rates and abundance. The second step count model utilized quantile regression to estimate the median abundance, a more robust statistic than the mean when analyzing species counts.

Before modeling, all data was split 75/25 into training/testing subsamples. Initial training data were further split 75/25 into training and out-of-bag samples for model validation (below). In non-event models, we also equalized weighting by year, accounting for the increasing sample sizes by year generated by eBird (submissions have increased roughly 30% every year since 2002). Finally, we randomly subsampled 25 000 records from the remaining checklists to reduce the computational burden. We repeated these processes and refit all models 25 times to reduce error generated by random subsampling and estimate uncertainty in estimates of occurrence and conditional abundance. For each model, we checked test–set calibration plots as a diagnostic of overfitting. Finally, we assessed the fit of each model based on a series of predictive performance metrics computed with the test data. The predictive performance metrics included specificity, sensitivity, Kappa and area under the curve (AUC).

To examine changes in occurrence and conditional abundance following extreme weather events, we began by calculating the partial dependence (Hastie et al. 2009) of the occurrence and conditional abundance on every date from 10 days prior to the event until 30 days after. These partial dependence statistics describe how occurrence and conditional abundance varied as a function of event date, averaging across the values of all other predictors in the occurrence and conditional abundance models across the event area. By averaging in this way, the partial dependence estimates capture systematic, area-wide changes associated with event date while averaging out all other sources of variation captured by the models, including variation in detection rates and heterogeneity in search effort and among observers.

To quantify species responses to the extreme weather events, we computed the ratios of the partial dependences before and after the event. Specifically, we divided the partial dependence for occurrence and conditional abundance at 5, 10 and 20 days following each event by the partial dependence averaged across the five days preceding the event. This ratio measures the relative change in species occurrence and conditional abundance before and after the event. Finally, to account for any typical seasonal movements in species' occurrence and conditional abundance, we computed the difference in seasonal shifts between the event and non-event years over identical calendar dates. The resulting metrics measure the proportional change in species occurrence and conditional abundance due to the events, after accounting for typical intra- and inter-annual changes. We further measured cross-species relationships between changes in conditional abundance and occurrence using simple linear regression.

Finally, we wished to determine how the magnitude of the anomalous shift in occurrence and conditional abundance following extreme weather events compared to equivalent shifts during years in which extreme events did not occur. This would help us further assess whether shifts following extreme weather fell outside of typical interannual cross-species fluctuations in occurrence and conditional abundance. We iteratively generated these cross-species metrics over the same dates for each year between 2011 and 2018 (years with > 5000 checklists over these dates) relative to all other years. For computational feasibility, we generated interannual metrics based on five (rather than 25) resampled model fits. As this produced some extreme values for several species in certain years, we present medians rather than means. Further, we limited the years that we iteratively compared to 2011–2017, as years prior to 2010 did not have > 10 000 records before and after extreme weather events and 2018 could not be analyzed because it would require 2019 checklist data, which we do not have access to.

To generate maps depicting change in predicted occurrence and conditional abundance throughout a species range before and after an extreme weather event, we created a gridded dataset with 2.8 km^2 resolution and generated predictions in each cell five days prior to an extreme event and 10 days after the event. To account for variation in detectability, we held all of the observation process predictors constant, resulting in occurrence predictions for a standardized eBird search defined as a checklist reported by an average observer traveling 1 km over one hour during the year of the event, at the hour of the day when a given species is most commonly observed, and on a day with mean 1970–2000 winter (Dec–Feb) temperatures and precipitation totals (obtained via Worldclim; Fick and Hijmans 2017). Predictions were generated using values of land cover, elevation and topographic predictors corresponding to each cell. We divided predictions following an extreme weather event by predictions before the event and then subtracted this value from similar changes in predictions from all other years to generate the plotted percentage change values. Maps were generated using the *purr* package (Henry and Wickham 2017) and plotted using *RColorBrewer* (Neuwirth and Neuwirth 2011). All plots visualizing partial effects and metrics were generated using *ggplot2* (Wickham 2011).

Cross-species models

The final step in our modeling process involved examining how shifts in occurrence and conditional abundance following extreme weather events across species were associated with various avian life-history traits. For all species, information on diet type and preferred habitat (categorical variables), and body mass (continuous) was collected from Barnagaud et al. (2017). We grouped several categories of each predictor to increase power. Diet type categories included carnivore, invertebrate, omnivore and herbivore (a combination of 'fruit', 'nectar', 'vegetation' and 'seed' in the original dataset). Habitat categories included water ('coastal', 'open_water'), open ('semi-open', 'rock', 'arid'), generalist ('urban', 'developed'), forest and riparian wetlands. Further, we calculated species-level landcover diversity index (LDI), a measure of habitat generalism, based on mean partial effects of all landcover covariates (following Zuckerberg et al. 2016). Finally, we calculated species thermal index (STI), a measure of the long-term mean temperature in a species range that indicates whether it is likely to be adapted to cool or warm weather, by taking the mean winter (Dec–Feb) daily minimum temperature across all points where a species was observed on a checklist between 2004 and 2018 (following Princé and Zuckerberg 2015). High collinearity between functional traits and phylogeny precluded us from testing for phylogenetic effects in occurrence and conditional abundance patterns.

We fit multivariate linear models (LMs) including all of the above traits as predictor variables to examine how traits predict species' responses following each extreme weather event. Models were fit separately for occurrence and conditional abundance responses. Following each LM, we employed a model selection approach in which we fit models with all possible combinations of predictor variables (via the MuMIn package; Barton 2014) to identify important predictors. LMs with all combinations of trait predictors were fit and predictors were scored by the proportion of model weight accounted for by models in which they were present. We evaluated whether the shifts in occurrence or abundance at 5, 10 or 20 days following each event were phylogenetically correlated by calculating Blomberg's K (Blomberg et al. 2003) using an avian phylogeny (Jetz et al. 2012) and comparing it to a null distribution of K after randomizing species' responses 1000 times ('picante' package; Kembel et al. 2010).

Results and discussion

Overall, bird species demonstrated highly distinct responses to the polar vortex and heat wave. Across all species, median conditional abundance typically decreased five and 10 days after the polar vortex relative to the five-day period before the polar vortex (−6.3% ± 1.7 SE and −5.5% ± 1.4, respectively, suggesting disaggregation), but returned to previous levels after 20 days (1.8% ± 2.1; Fig. 2b). Meanwhile, occurrence rates on average remained relatively stable following the polar vortex (5d: −1.6% ± 1.5; 10d: −0.8% ± 1.1; Fig. 2a). Following the heat wave, both median occurrence

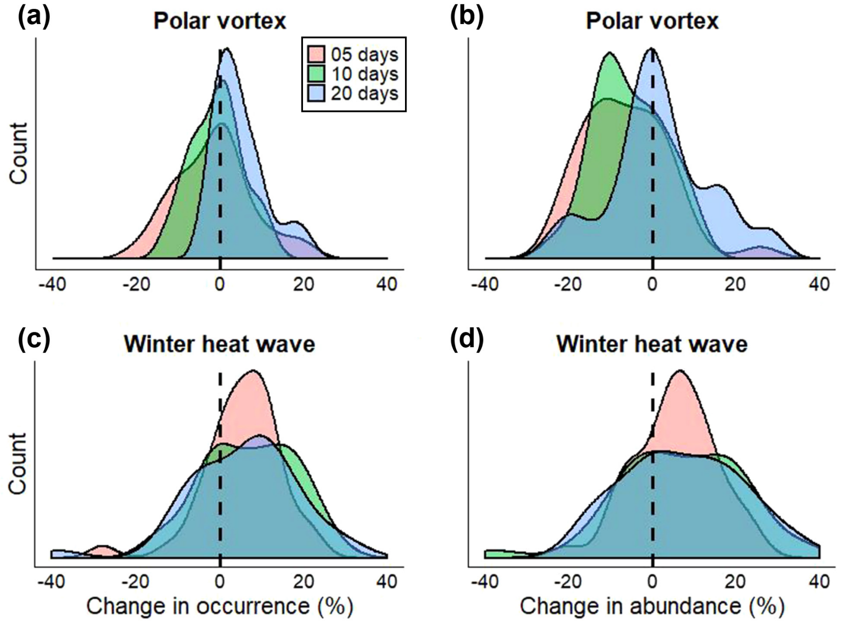

Figure 2. Responses to extreme weather events across avian species. Density plots show percent changes in occurrence (a, c) and conditional abundance (b, d) at various time points following the 2014 polar vortex (a, b) and 2015 winter heat wave (c, d). Percent changes given are the change following a five day period before each event subtracted from the change over an identical period during other winters. Colors represent time points following each event: 5 days (red), 10 days (green) or 20 days (blue). On average, species decreased their conditional abundance but not occurrence following the polar vortex, and increased both their occurrence and conditional abundance following the heat wave.

and conditional abundance probabilities increased at all time points for most species (occurrence: 5.2% ± 1.4, 6.6% ± 2.2 and 5.4% ± 2.0 at days 5, 10 and 20, respectively; conditional abundance: 5.3% ± 1.5, 6.4% ± 2.3 and 5.7% ± 2.4; Fig. 2c-d). Occurrence and conditional abundance changes remained synchronized five days after the polar vortex ($R^2 = 0.66$; $\beta = 0.72 \pm 0.09$), although these relationships decoupled after 10 and 20 days ($R^2 = 0.17$, 0.06; $\beta = 0.30 \pm 0.12$, 0.13 ± 0.08, respectively) due to a much stronger effect of the polar vortex on bird conditional abundance than occurrence. However, the heat wave synchronized changes in occurrence and conditional abundance ($R^2 = 0.84$, 0.89, 0.80; $\beta = 0.88 \pm 0.06$, 0.91 ± 0.05, 0.74 ± 0.06; Supporting information). At the species level, there was a negative relationship between the immediate response to the two winter weather events; bird species that increased in occurrence or conditional abundance following the polar vortex were most likely to decline in occurrence or conditional abundance following the heat wave, and vice versa (5d change in occurrence: $\beta = -0.70 \pm 0.12$; conditional abundance: $\beta = -0.46 \pm 0.13$; Fig. 3). However, we observed the reversed pattern 20 days after the weather events – species shifted their occurrence probabilities, though not median conditional abundance, at similar rates to both weather events (5d change in occurrence: $\beta = 0.61 \pm 0.37$; conditional abundance: $\beta = 0.18 \pm 0.55$; Fig. 3). The magnitude of cross-species shifts in conditional abundance (and for the heat wave, occurrence) exceeded analogous shifts over equivalent time periods during other years, when extreme weather did not occur (Supporting information), suggesting that the observed responses fall outside of the typical inter-annual cross-species variation in occurrence and conditional abundance.

At the species level, responses to extreme weather events hinged on functional traits, notably distribution, body size and habitat preference (Supporting information). As expected, warm-adapted species were more likely than cold-adapted species to decline in occurrence (Relative Importance score > 0.99; $\beta = -3.21 \pm 1.1$; henceforth, only top model coefficients are reported; Fig. 4b, Supporting information for model adjusted-R^2 values) and conditional abundance (RI = 0.96; $\beta = -2.57 \pm 1.55$; Supporting information) five days after the polar vortex, though this effect disappeared later. Five days after the polar vortex, cold-adapted species demonstrated only minor shifts in occurrence and conditional abundance by an average of +1.2% and −1.9%, respectively, whereas warm-adapted species declined by −4.6% and −10.7%. Following the winter heat wave, warm-adapted birds experienced average increases in occurrence of 9.2% (5d RI = 1; $\beta = 2.54 \pm 0.77$; Fig. 4e, Supporting information) and increased in conditional abundance by 8.5% (5d RI = 0.99; $\beta = 1.72 \pm 0.88$; Supporting information) in contrast with cold-adapted species, which increased by only 1.6% and 2.9%, respectively (Fig. 4d–f). Soon after the polar vortex, smaller-bodied species (those with below-average body size) decreased in occurrence and conditional abundance by an average of −6.8% and −10.0%, respectively, though body size was only an important predictor driving occurrence changes (occurrence: 5d RI > 0.99; $\beta = 1.25 \pm 1.24$; Fig. 5a, Supporting information; conditional abundance: 5d RI = 0.22; Supporting information); however, these effects diminished after twenty days. Meanwhile, larger-bodied species increased in occurrence by 3.6% and decreased in conditional abundance −3.0% following the polar vortex. After the heat wave, smaller-bodied species increased in occurrence by 8.4% and in conditional abundance 8.3%, while

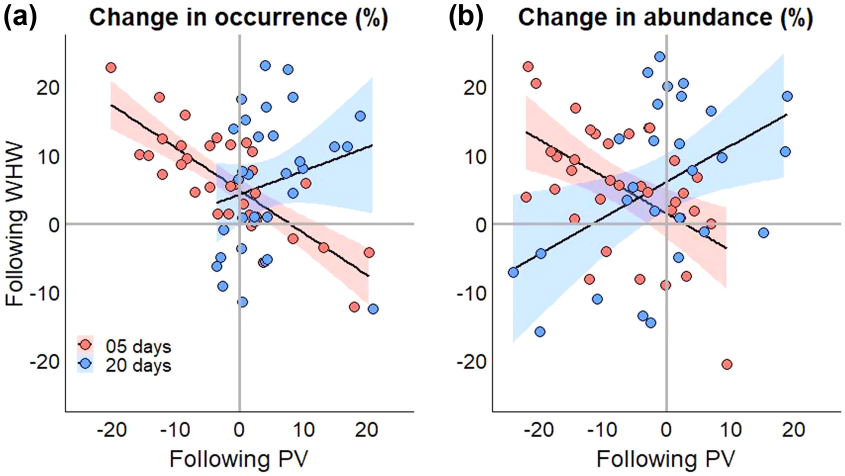

Figure 3. Species demonstrate opposite responses immediately following a polar vortex (PV) and winter heat wave (WHW). The figure demonstrates the relationship between percent changes in occurrence (a) and conditional abundance (b) at two time points following a polar vortex (x-axis) and winter heat wave (y-axis) at the species level (points represent individual species). Percent changes given are the change following a five day period before each event subtracted from the change over an identical period during other winters. Colored points and 95% confidence intervals represent time points following each event: 5 days (red) or 20 days (blue). Immediately (5 days) following both extreme events, bird species demonstrated opposite changes in occurrence and conditional abundance, but at longer time lags (20 days), birds responded similarly to the polar vortex and heat wave.

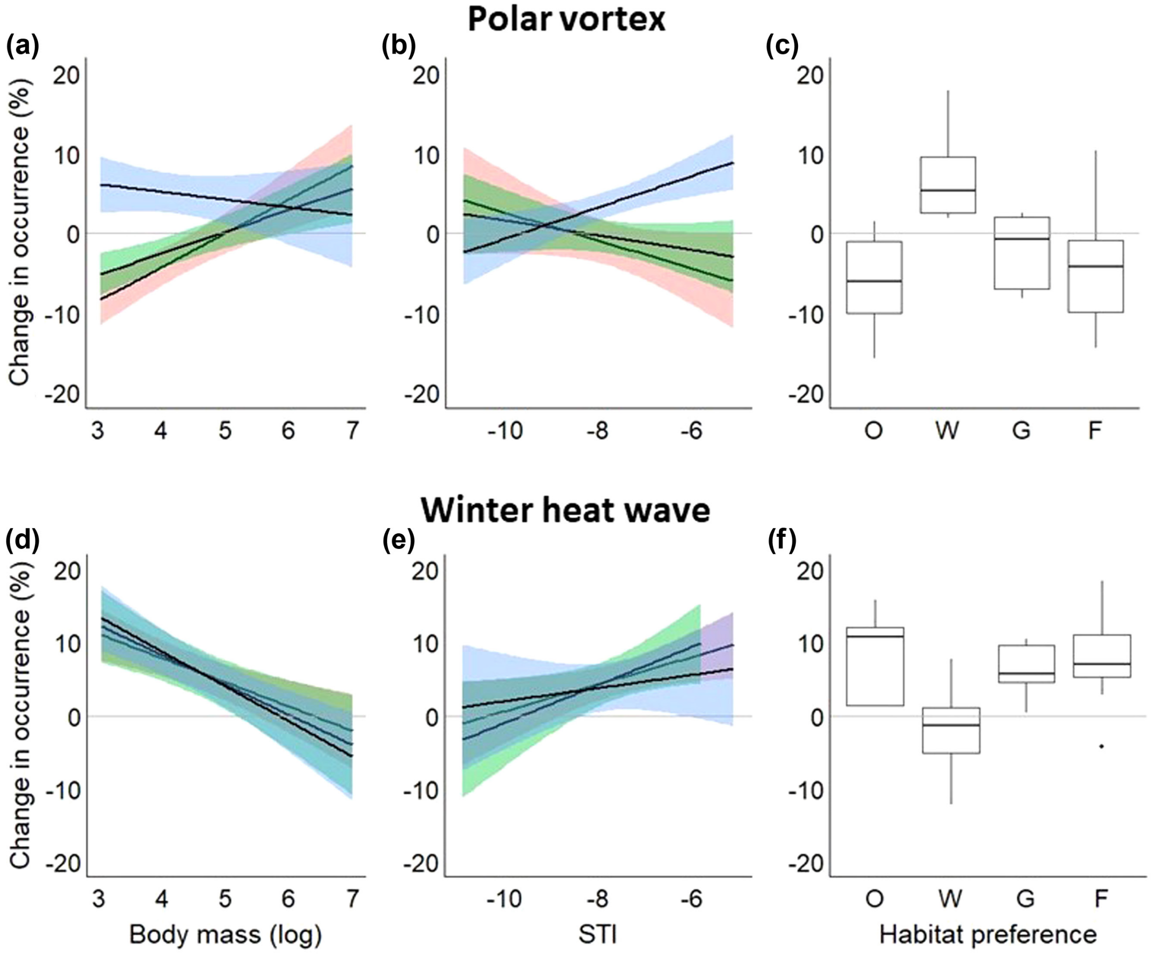

Figure 4. Functional trait groups demonstrate opposite responses to a polar vortex and winter heat wave. Following the 2014 polar vortex, species with smaller log-transformed body mass (a), greater species thermal index (STI; b) or species other than waterbirds (c; response at 5d shown) were most likely to decrease in occurrence. Conversely, following the 2015 winter heat wave, species with larger body mass (d), lower STI (e) or waterbirds (f) were most likely to decrease in occurrence. Percent changes given are the change following a five day period before each event subtracted from the change over an identical period during other winters. Colored 95% confidence intervals (a–b, d–e) represent time points following each event: 5 days (red), 10 days (green) or 20 days (blue). Habitat categories are as follows: O = open; W = water; G = generalist; F = forest.

larger-bodied species increased in each by only 1.6% (Fig. 4d, Supporting information). Consequently, warm-adapted and smaller-bodied species appeared to be more sensitive to both extreme events.

Five days after the polar vortex, only waterbirds (e.g. common goldeneye, *Bucephala clangula* and common merganser, *Mergus merganser*) on average increased in occurrence 7.1% despite decreasing in conditional abundance by −3.4%, while other species decreased by −4.1% and −7.2%, respectively, though habitat association was unimportant in model selection (Fig. 4c; Supporting information). However, following the heat wave, waterbirds initially declined in occurrence by −4.2% (5d RI = 1) and conditional abundance by −5.5% (5d RI = 1) while all other habitat groups increased by 8.5% and 8.9%, respectively (Fig. 4e; Supporting information). We did not observe that other functional traits greatly influenced species responses to extreme weather events (Supporting information). Maps predicted changes in occurrence probability and median conditional abundance of up to between −20% and 20%, depending on species and location (Fig. 5). Blomberg's K was never significantly different from what would be expected by chance (all p-values > 0.15; Supporting information), suggesting that species' responses were not phylogenetically correlated.

Our results suggest that on average, birds exhibited opposite responses soon (5–10 days) after the 2014 polar vortex and 2015 winter heat wave. Following the polar vortex, we observed consistent decreases in conditional abundance, but not occurrence, across most species. A temporary decline in conditional abundance, but not occurrence, after the polar vortex suggests that birds may be spreading out to seek out refugia or dwindling resources (Borregaard and Rahbek 2010) or temporarily left the affected area (e.g. moved south), and were thus often observed in lower numbers by eBird users. These responses were generally short-lived; thus, the responses likely reflected behavioral changes and were

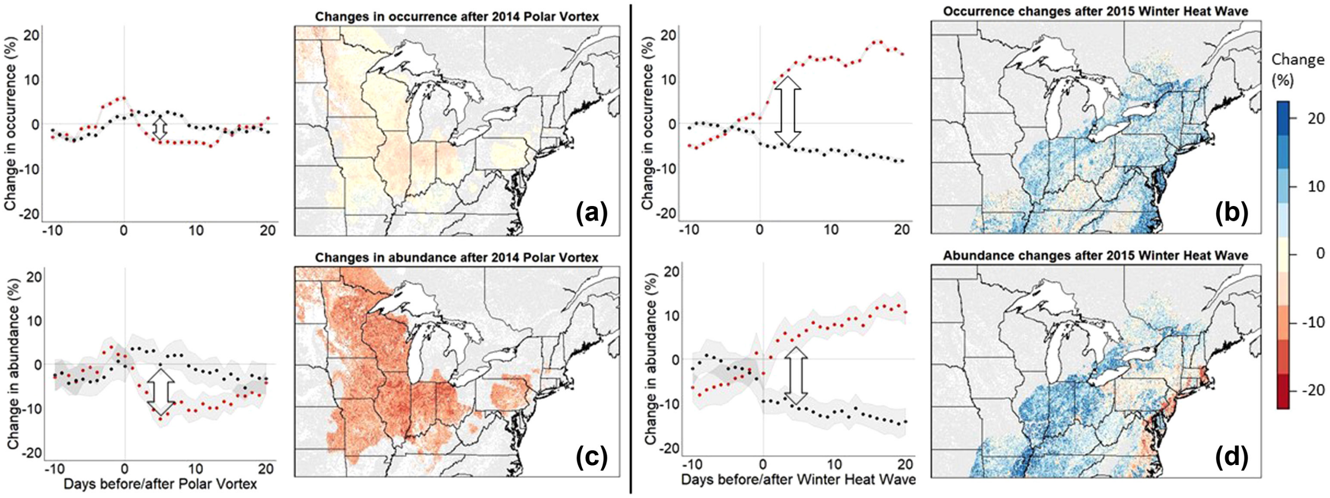

Figure 5. Responses of mourning doves *Zenaida macroura* to the 2014 polar vortex and 2015 winter heat wave. Percent changes in occurrence (a, b) and conditional abundance (c, d) following the 2014 polar vortex (a, c) and winter heat wave (b, d) are shown for mourning doves. Partial dependence plots show partial effect means and 95% CIs (across 25 model runs) in occurrence or conditional abundance before and after each weather event (day 0); red points represent predictions generated before and after the weather event, and black points represent predictions for all other non-event years between 2004 and 2018. Maps display percent changes five days following the weather event (bidirectional arrows in partial dependence plots) relative to the five day mean beforehand, adjusted to account for typical trends over these dates. Colored regions of maps represent portions of the species range that experienced less than −10°C shifts for at least four days during the weather event. Gray areas show the remainder of the species range. Bluer colors signify percent increases, redder colors are decreases and beige areas represent no change.

unlikely to carry long-term consequences for most species. In contrast, birds responded to the heat wave by increasing in both occurrence and conditional abundance for at least 30 days, suggesting birds may have increased their behavioral activity (e.g. time spent feeding) and were therefore more noticeable to contributors submitting checklists. Some species may have even shifted their ranges northwards, either temporarily or through the winter, appearing on more checklists because they became more common in the area affected by the heat wave. Recent evidence suggests that, as a result of a warming winter climate, resident birds (including most of those tested) are responding more strongly than other bird groups by shifting northward and colonizing new areas along northern leading edge of their breeding ranges (La Sorte and Thompson 2007, Rushing et al. 2020).

Although we did not directly test for changes in the total number of individuals after extreme weather events, overall increases in both occurrence and population density (measured via conditional abundance) following the heat wave suggest that the number of individuals in the affected area likely increased. Likewise, cross-species trends demonstrating stable occurrence rates despite decreases in population density following the polar vortex imply a possible decrease in the number of individuals in the affected area. However, given that conditional abundance for most species recovered to previous levels about 20 days following the polar vortex, our results do not suggest that these extreme weather events strongly impacted the survival of most species tested. Interestingly, the lack of response in occurrence rates for most species following the polar vortex likely caused a decoupling in abundance–occupancy relationships for many species following this event, but not following the heat wave. A positive relationship between occurrence and abundance is pervasive throughout macroecology with important implications in conservation biology (Gaston 1996, Gaston et al. 2000). In this case, a breakdown in abundance–occupancy relationships across species due to an extreme weather event suggests that varying sensitivity of species to climate variability may be an important, albeit understudied, mechanism underlying this macroecological pattern.

Much of the species-level variation in responses to each extreme weather event was associated with several key functional traits. For example, smaller-bodied birds strongly reduced their occurrence following the polar vortex and greatly increased their occurrence and population density after the heat wave, while larger-bodied birds exhibited more muted shifts in response to each event, possibly because they have greater thermal inertia (Huey et al. 2012, Albright et al. 2017) and may thus be less impacted by short-term temperature changes. Further, we observed that warm-adapted species were most likely to decrease in population density following a polar vortex and most likely to increase in occurrence and population density after a heat wave, while cold-adapted species were much more resilient to each event. Finally, although we predicted birds occupying open areas to be more sensitive to extreme weather, we found that waterbirds reacted differently than other birds. Waterbirds occurred more often following the polar vortex and less often after the heat wave, while other species demonstrated opposite shifts. Because most of the larger-bodied species we analyzed were also waterbirds, it was not possible to separate the influence of functional traits from each other.

However, at minimum we can conclude that large-bodied waterbirds (mostly Anseriformes) appeared to be far less sensitive to a polar vortex than smaller-bodied passerines, but may also experience smaller increases in population density and occurrence following a winter heat wave.

Our results shed light on how species respond to two types of extreme winter weather events that are increasing in frequency and intensity with climate change, a polar vortex and winter heat wave. However, it remains unclear how species respond to extreme weather events during other periods of the year. For example, birds may be highly vulnerable to extreme weather during the breeding season as they have high energetic requirements and cannot easily relocate when they are caring for young (Conradie et al. 2019, Cohen et al. 2020). Further, if juveniles have especially high susceptibility to extreme weather, breeding season weather events could carry long-term demographic consequences for populations (Bourne et al. 2020). Extreme weather occurring on the shoulder seasons, spring and autumn, may leave migrants exposed to conditions they cannot tolerate. For example, a freeze or snowfall occurring early in autumn or late in spring could leave neotropical migrants exposed to cold weather that they rarely experience under typical circumstances (Casson et al. 2019), and may alter insect phenology (Sevenello et al. 2020) or damage plants, fruit and seeds (Kunkel et al. 2013), possibly leaving these species without food sources needed to fuel continental-scale migrations or hampering breeding success (Krause et al. 2016). Thus, extreme weather during shoulder seasons could result in greater mortality than mid-winter extreme weather events, which exclusively affect winter residents that are likely to be tolerant of a broader range of thermal conditions than neotropical migrants (Somveille et al. 2015, 2019). Alternatively, mid-winter extreme weather events involving precipitation, such as rain-on-snow events in which rapid freezing and unfreezing causes very high ice accumulation, may result in mortality because they can destroy habitat, make microclimate (e.g. snowpack) inaccessible or block food sources (Putkonen and Roe 2003, Casson et al. 2019). Further work is needed to determine how species respond to additional forms of extreme weather throughout the annual cycle.

Climate sensitivity is a key facet of assessing species vulnerability to climate change and reflects whether certain species are more susceptible to the effects of climate variability due to differences in physiology, habitat specialization or other life history characteristics (Moritz and Agudo 2013). By measuring the responses of temperate-wintering birds to short-term climate variability over a broad geographic scale, we offer a robust and novel estimation of sensitivity that could be incorporated in future assessments of climate change vulnerability (Rapacciuolo et al. 2012). Integrating citizen science and machine learning provided a framework for calculating partial dependencies, mapping species-level responses to extreme weather across a broad geographic region and identifying which species are more vulnerable. Failing to account for the multi-scale structure of these species-level responses may produce unreliable estimates of which species are most likely to be impacted by future climate change (Oedekoven et al. 2017).

Here, we took advantage of a natural experiment to quantify how 41 common North American bird species shifted in occurrence and conditional abundance in response to two extreme weather events, an intrusion of a polar vortex and a winter heat wave, using high-resolution citizen science data continuously recorded before and after each event. Our results suggest that extreme weather events, despite lasting only several days, are likely to greatly impact the behavior and distribution of birds but unlikely to do so in a consistent manner. Future work is needed to determine if long-term range shifts, one of the hallmarks of ecological responses to modern climate change, can result from a single extreme weather event. With extreme winter weather becoming more common, it will be critical for researchers and managers to better understand how birds respond to extreme weather events and to determine which species are most likely to be vulnerable.

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Author contributions

Jeremy Cohen: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Daniel Fink**: Conceptualization (equal); Data curation (equal); Resources (equal); Supervision (equal); Visualization (supporting); Writing – review and editing (equal). **Benjamin Zuckerberg**: Conceptualization (equal); Funding acquisition (lead); Supervision (equal); Writing – review and editing (equal).

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Data sharing and accessibility

eBird data is available for public use online at <https://ebird.org/science/download-ebird-data-products>. Code generated to conduct the analyses is available upon request.

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