



A North American climate-masting-irruption teleconnection and its change under future climate

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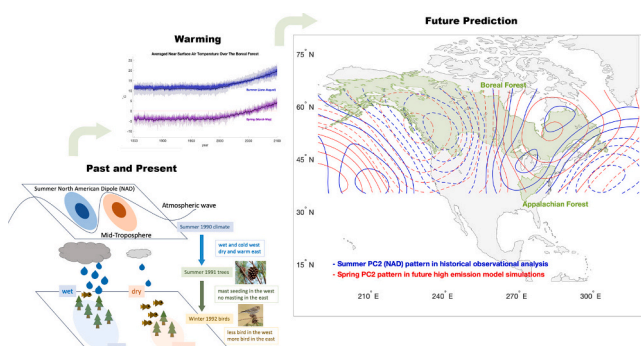
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HIGHLIGHTS

- The first test of the bird irruption mechanism using mast seeding data
- Projected climate change shifts the North American Dipole from its current summer timing to spring.
- This discovery provides far-reaching impacts on studying boreal forests and their associated species.

GRAPHICAL ABSTRACT



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ABSTRACT

Atmospheric variability can impact biological populations by triggering facultative migrations, but the stability of these atmosphere-biosphere connections may be vulnerable to climate change. As an example, we consider the leading mode of continental-scale facultative migration of Pine Siskins, where the associated ecological mechanism is changes in resource availability, with a mechanistic pathway of climate conditions affecting mast seeding patterns in trees which in turn drive bird migration. The three summers prior to pine siskin irruption feature an alternating west-east mast-seeding dipole in conifer trees with opposite anomalies over western and eastern North America. The climate driver of this west-east mast-seeding dipole, referred to as the North American Dipole, occurs during summer in the historical record, but shifts to spring in response to future climate warming during this century in a majority of global climate models. Identification of future changes in the timing of the climate driver of boreal forest mast seeding have broadly important implications for the dynamics of forest ecosystems.

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1. Introduction

The spatial extent of climate patterns synchronize ecological processes over local to regional scales, a phenomenon referred to as the Moran effect (Moran, 1949). Consequently, species abundance, and the survival and reproduction of individuals within geographically disjunct populations may be synchronized by regional environmental conditions. However, at broader scales, emerging research highlights a tendency for ecological processes to subsequently anticorrelate, forming what are now known as ecological dipoles – fluctuations in ecological responses that are of opposite polarity (antisynchronized) and separated by large geographic distances (Zuckerberg et al., 2020; LaMontagne et al., 2020).

Ecological dipoles are likely to be common, as atmospheric Rossby waves organize continental-scale climate variability into juxtaposed regions of oppositely-signed anomalies (Madden, 2007; Bai, 2022). Modes of climate variability are dynamic environmental drivers, with temperature and precipitation fluctuations capable of synchronizing ecological processes (Stenseth et al., 2002). When Rossby waves lead to dipoles in climate anomalies, for example, North America's western boreal forest might have an anomalously warm and dry summer while the eastern forest is anomalously cool and wet, ecological processes within regional populations can synchronize to the climate's geographic scale and periodicity (Ascoli et al., 2021; Pomara and Zuckerberg, 2017). The North American Dipole (NAD) is a significant mode of summer atmospheric circulation variability (magenta contours in Fig. 1c), and has been identified as the key factor influencing the occurrence of the North American mast seeding-irruption dipoles (Bai et al., 2023). This ecologically relevant NAD pattern, driven by atmospheric teleconnection, is often triggered by the tropical and monsoonal storminess over ocean basins upstream from the affected continent (Bai

et al., 2023; Bai and Strong, 2023). This indicates that fluctuations in climate variability initiated by remote conditions affects population demography in a suite of species at continental scale, ultimately imparting periodicity on ecological processes across ecosystems (Zuckerberg et al., 2020; Stenseth et al., 2002).

An exemplary ecological dipole that demonstrates the interconnectedness of climate variability and resource dynamics is the impact of climate on spatiotemporal patterns of mast seeding of trees in the boreal forest, and associated triggering of boreal bird irruptions. Irruption is a form of facultative migration, in which many individual birds travel outside of their normal range; it is often theorized to be driven by geographically synchronized fluctuations in food supply (Newton, 2012). Pine siskins (*Spinus pinus*) in particular exhibit a West-East Mode (WEM) of irruption over the boreal forest which has lagged correlations with continental-scale antecedent climate anomalies (Strong et al., 2015). Positive values of the WEM correspond to anomalously high Pine Siskin counts over the eastern forest with low counts to the west, and negative values of WEM index correspond to the reverse (Fig. 1a). The WEM index is significantly correlated with the North American Dipole (NAD) index with NAD leading WEM by three summers ($r = 0.58$, $p < 0.01$; Fig. 1b). The associated mechanism underlying these irruptive movements is thought to be climate-associated anomalies in seed production which are highly temporally variable and highly synchronous at regional scales (referred to as “mast seeding” or “masting” (Silvertown, 1980; Kelly, 1994)), and is antisynchronized across continental scales (LaMontagne et al., 2020). The seed-crop failure hypothesis theorizes that irruption is driven by the broad-scale reduction in resource variability resulting from widespread failure of seed production following a synchronized pulse of seed production during a mast-seeding event (Strong et al., 2015). Previous work supports the

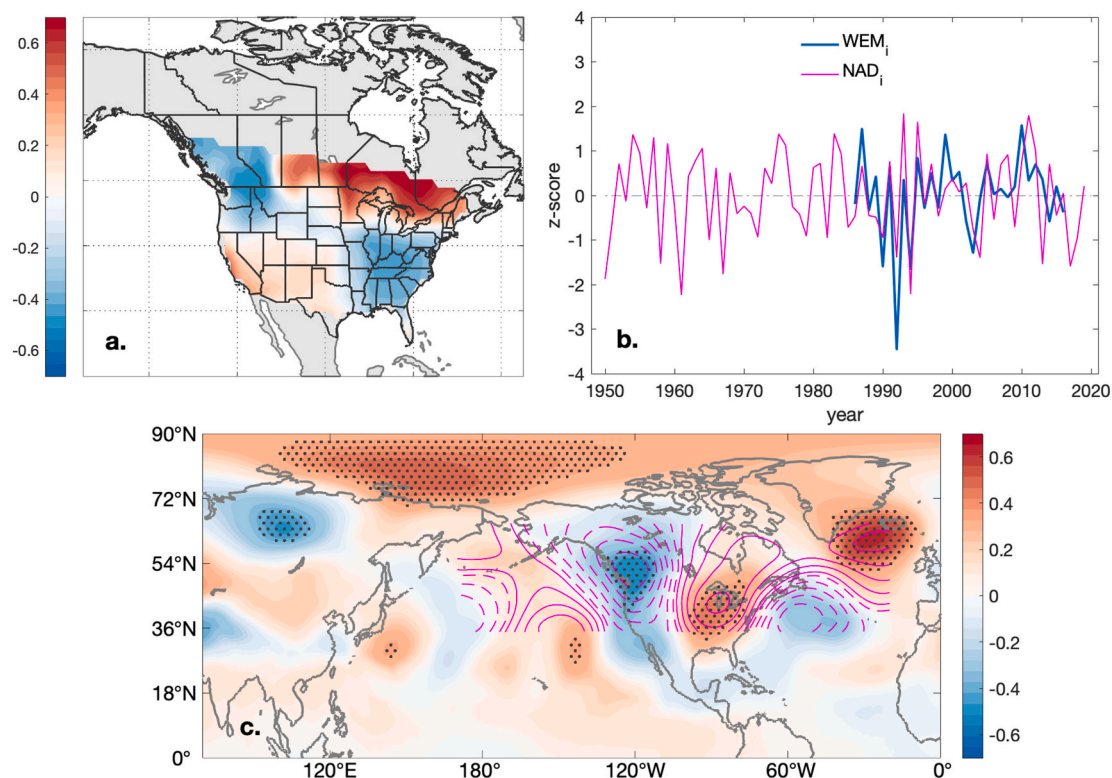


Fig. 1. The West-East irruption mode (WEM). (a) WEM spatial pattern shown by the correlation between the WEM index (WEM_i) and pine siskin counts, where the WEM_i is the second principal component of pine siskin counts. (b) Time series indices of the WEM index (WEM_i) and North American Dipole index (NAD_i) derived from ERA5 data covering 1950–2019; the WEM_i is shifted to the left on the figure to remove its two-year lag with the NAD_i. (c) Lagged correlation between WEM_i and June–August mean 500-hPa geopotential height (Z₅₀₀) in ERA5 (shading), and the spatial pattern of the NAD (magenta contours with negative value dashed and zero contour suppressed). For the shaded correlation, the geopotential height data (1986–2016) led the bird data (1989–2019) to account for the lags associated with the development timeline for conifer seeds and bird migration. Stippling indicates statistical significance at the 95 % confidence level.

localized association between annual seed variability and facultative migration of birds outside of their resident ranges in search of food (Koenig and Knops, 2001; Bock and Lepthien, 1976).

Current and future climate change threaten the ecological function of ecosystems globally, and while increasing trends in temperature receive much focus, climate variability is critical in mediating the periodicity of ecological processes. Year-to-year changes in temperature significantly impact the initiation of mast seeding in trees (Kelly et al., 2013), potentially outweighing the importance of warming trends in the pattern of temporal variability in mast seeding over time (LaMontagne et al., 2021). We theorize that future changes in the climate variability, beyond those of warming, will impact modes of resource variability through seed production and associated ecological teleconnections.

Here, we explore the development of a climate-resource-migration dipole leveraging seasonal weather, a continental database of seed production in conifer trees, and bird observations from an international community science effort to investigate how associated atmospheric drivers will evolve under projected climate change. We hypothesize that future climate projections include not just overall warming, but more-over changes in the geography and timing of climate dipoles relevant to masting-irruption dynamics. To test the hypothesis, we focus on the NAD as a key driver of continental antisynchrony of mast-seeding, and detect in what season the NAD occurs in future warming scenarios simulated by Global Climate Models (GCMs).

2. Data and methods

2.1. Bird data

The magnitude and periodicity of bird irruptions were analyzed using observations collected during Project FeederWatch (PFW) (Bonter and Hochachka, 2009). Pine siskin counts consist of a 2-day observation period separated by 5 days and begin on the second Saturday in November and run for 21 weeks during the winter. We totaled the bird counts over that period for each site and year in which the collection period ended (e.g., FeederWatch year 1989 corresponds to November 1988 through April 1989). PFW has been collecting data since 1989 and over 25,000 participants regularly enlist annually across the United States and Canada (Zuckerberg et al., 2011, 2012). We chose Pine Siskins as focal species, because they are one of the most visible and widespread North American seed-eating birds and they also engage in irruptive movements (Watts et al., 2017). Data for 1989–2019 were analyzed to obtain the West-East Mode (WEM) spatial pattern and index following the methods detailed in our prior work (Strong et al., 2015; Bai et al., 2023).

2.2. Seed data

Data on annual conifer seed production were primarily obtained from the MASTREE+ mast-seeding database (Hackett-Pain et al., 2022), and we extracted data focusing on Canada and the continental United States; the analysis period is 1987–2019, overlapping the bird records. We synthesized data from the family Pinaceae including *Abies* spp., *Picea* spp., and *Tsuga* spp. ($n = 711$ time series) to investigate the lagged correlation between bird irruption and the impacts of the climate dipole. *Pinus* spp. data were excluded because the seed-development time is longer for *Pinus* spp., which spans 3 years as opposed to 2 years. Additionally, *Pinus* spp. exhibit lower variability in their annual patterns of seed production compared to other Pinaceae species with two-year seed development times, as noted by LaMontagne et al. (2021). This lower temporal variability means that the fluctuations between high and low seed production values are less extreme than in other Pinaceae species with two-year seed-development times. Following this exclusion, we still had data from more than 700 sites, allowing us to produce robust results. Therefore, we decided that performing and presenting a separate parallel analysis for *Pinus* spp. was not necessary. Here we also note that

pine siskins are not *Pinus* specialists per se. During the winter, they predominantly consume small seeds from conifers such as spruce, red alder, and birch. To be included in the analysis, the time series length was a minimum of six years, and data from each time series were standardized to values between 0 and 100 before analysis.

2.3. Climate data

All data described here were detrended prior to any calculations. For analysis of historical atmospheric variability, we used reanalysis data from 1950 to 2019 for monthly averaged 500-hPa geopotential height (Z_{500}) from the European Centre for Medium Range Weather Forecasts (ECMWF) Reanalysis (ERA5) on a 30-km grid (Hersbach et al., 2020). For future climate, we used simulations performed for the Coupled Model Intercomparison Project phase 6 (CMIP6) (Eyring et al., 2016a). For each model, we analyzed its historical run (1850–2014) and future run (to 2100) based on a high emission scenario (Shared Socioeconomic Pathway 5–8.5; SSP585). Fourteen models were selected as having the strongest correlation between their historical summer NAD pattern and the observed summer NAD pattern (Supplementary Table A.1).

2.4. Principal component analysis (PCA)

In this research, the variability patterns were examined through the application of principal component analysis (PCA), also known as empirical orthogonal function (EOF) analysis (Hannachi et al., 2007). All data were detrended prior to performing the PCA.

As in our prior work, the NAD was defined as the second principal component (PC2) of 500-hPa geopotential height in the domain 35°–65°N, 170°–340°E. The observed historical NAD was derived from ERA5 data averaged over June–August over the years 1950–2019 (Bai et al., 2023). The spatial pattern of the NAD is the eigenvectors of the spatial covariance matrix (magenta contours, Fig. 1c). The NAD index (NAD_i) time series was produced by projecting the centered data onto the NAD spatial pattern (magenta curve, Fig. 1b).

Also following our prior work, the West-East Mode (WEM) of pine siskin irruption was defined as PC2 of PFW bird counts over the years 1989–2019. The spatial domain for the analysis is the shaded region in Fig. 1a. The spatial pattern of the WEM is the second eigenvector of the spatial covariance matrix, illustrated by the correlation between bird counts and the WEM in Fig. 1a. The associated WEM_i index is the centered bird count data projected onto the WEM spatial patterns (blue curve in Fig. 1b).

For the CMIP6 simulations, we inspected PC2 over the NAD domain in each model's historical run and future SSP585 run separately for spring (March–May) and summer (June–August). The sign of a PC is arbitrary and was reversed to ensure positive correlation between the simulated and observed NAD. The model and observed NAD patterns were then interpolated onto a standard grid of $2.5^\circ \times 2.5^\circ$ to calculate their spatial correlations. Spatial correlations were calculated between the observed historical NAD and the three patterns – the model's historical spring PC2, future spring PC2, and future summer PC2 (these are the values indicated by bars in Fig. 4).

3. Results

The three summers prior to pine siskin irruption feature a strong west-east conifer mast-seeding dipole over North America which reverses in sign each summer (Fig. 2), supporting the following masting-irruption chronology. Two summers prior to west-to-east irruptive migration, there is enhanced conifer masting over the western boreal forest (red shading, Fig. 2b) promoting a large pine siskin population in this region, and lower seed production over the eastern boreal forest (blue shading, Fig. 2b). The reverse patterns occur during the following summer (shading, Fig. 2a), and the large population migrates toward enhanced masting in the eastern boreal forest (red shading, Fig. 2a).

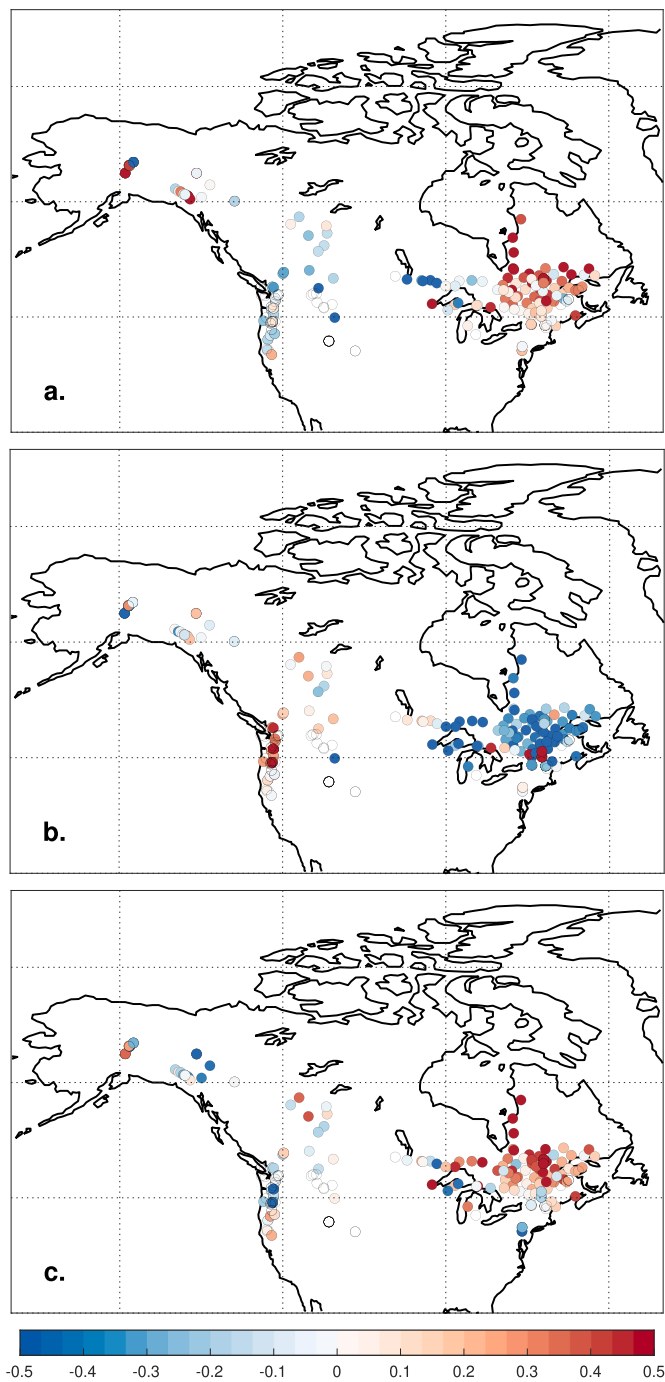


Fig. 2. Mast seeding associated with West-East irruption mode. Lagged correlations between summer conifer mast seeding and WEM_i in pine siskin, where mast seeding leads the WEM_i by (a) one year, (b) two years, and (c) three years. Note that the FeederWatch year is from November to March, so as an example, the one-year lag in (a) corresponds to pine siskin data from 1989 to 2019 correlated with conifer mast seeding data from 1988 to 2018. Marker represents the location of the mast-seeding time series.

While the mast seeding anomalies driving the WEM are apparent during two prior summers, the similarity of the lagged correlation results in Fig. 2a, c illustrates that the WEM tends to follow a reversing sequence of mast seeding anomalies lasting at least three years, rather than a two-summer sequence occurring in isolation.

The mast seeding-irruption-climatology described above is closely linked to climate variability, in particular the NAD pattern highlighted in our prior work (Bai, 2022). Positive NAD produces warm and dry conditions

over the eastern boreal forest, and cool and wet conditions over the western boreal forest (Supplementary Fig. A.6). This means that positive NAD during a given summer leads to anomalously high seed production over the eastern boreal forest, and anomalously low seed production over the western boreal forest, during the subsequent summer as shown by the lag-1 correlation in Supplementary Fig. A.5. This explains the positive lag-2 correlation between the WEM and NAD (Fig. 1b), consistent with the following climate-masting-irruption chronology. Positive WEM occurs three years after the NAD switches from negative to positive because negative NAD three years prior to irruption produces a high-west/low-east masting pattern (Fig. 2b), and then a subsequent positive NAD two years prior to irruption produces a high-east/low-west mast seeding pattern (Fig. 2a). Likewise, negative WEM occurs three years after the NAD switches from positive to negative. The role of NAD sign reversal as a climate driver of the WEM appears critical here, but we note that there is a complementary effect provided by the tendency for mast seeding anomalies to reverse sign year to year because trees presumably must replenish their reserves after a mast year (Satake and Iwasa, 2000) and mast-seeding events do not occur in consecutive years (LaMontagne and Boutin, 2009).

Observational identification of this climate-masting-irruption mechanism enables us to investigate how it will evolve under projected climate change using simulations from the most recent Coupled Model Intercomparison Project (CMIP6) (Eyring et al., 2016b). From prior work, the climate mechanism driving the west-east mast seeding pattern described above is the North American Dipole (NAD). In historical observations, the NAD appears as the second principal component (PC2) of geopotential height in the North American sector, featuring a prominent west-east dipole over North America (magenta contours, Fig. 1c). A central result here is that the NAD shifts from its current summer timing to spring in response to warming projected for this century under a high greenhouse gas emission scenario. We first illustrate this for one global climate model, and then show it is a change common to most models.

In the historical simulation (1850–2014) from one example model, the NAD appears as PC2 during summer (Fig. 3b), as seen in observations. This simulated mode accounts for 13 % of the geopotential height variance and is significantly spatially correlated with the observed NAD pattern ($r = 0.8$). We note that the PC2 pattern during spring differs from the NAD in observations and simulations, featuring a monopole pattern over North America (e.g., Fig. 3a) rather than the NAD's dipole pattern. When we examine PC2 in this example model's future simulation, we find the NAD shifted to spring (Fig. 3c) with a pattern no longer resembling the NAD during summer (Fig. 3d). The future spring NAD accounts for 17 % of variance and is significantly spatially correlated with the observed NAD ($r = 0.54$; Fig. 3c). For completeness, we check the leading principal component and find it to be distinct from the NAD during historical and future spring and summer (Supplementary Fig. A.9, columns 1 and 3). For connection to prior work on the climate anomalies associated with the NAD, temperature and precipitation anomalies associated with the patterns in Fig. 3 are shown in Supplementary Figs. A.7 and A.8.

To explore the potential generality of the above finding, from CMIP6 we select 14 models that best captured the NAD in their historical simulations (blue bars in Fig. 4). Strikingly, for approximately two thirds of these models (9 out of 14), the high greenhouse gas emission scenario shifts the future NAD pattern a season earlier, from summer to spring. This is illustrated by the red and green bars in Fig. 4, which show the spatial correlation between the historical observed summer NAD and each model's future spring PC2 (red bars) or summer PC2 (green bars). For 9 of the 14 models, the future spring PC2 spatial pattern correlates with historical NAD better than the future summer PC2, similar to the change shown in detail for one model above. For four of the models, the correlation is around twice as strong for spring versus summer (BCC-CSM2-MR, NorESM2-MM, ACCESS-CM2, and ACCESS-ESM1-5). Considering the climate-ecosystem implications of the NAD-WEM

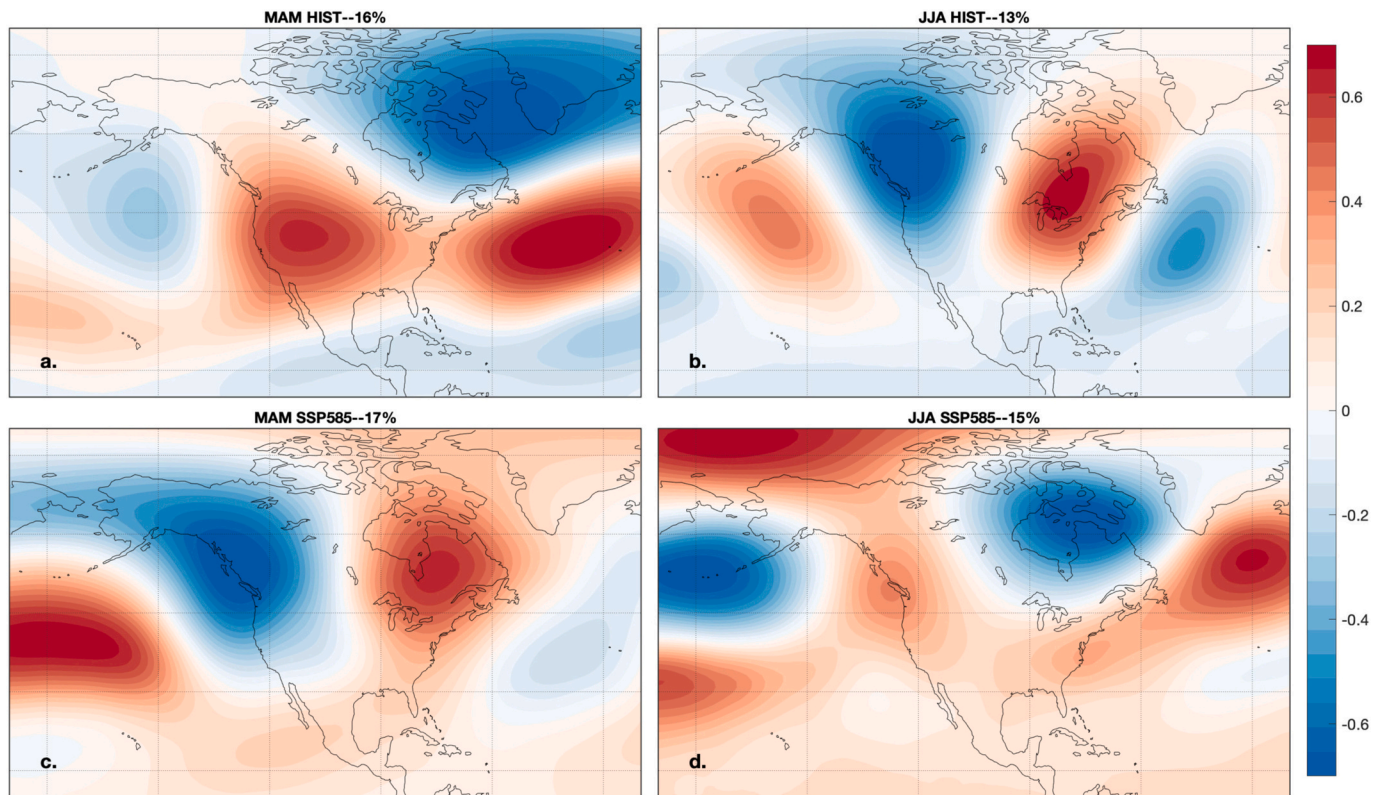


Fig. 3. Model circulation patterns. For one example CMIP6 model (BCC-CSM2-MR), the spatial pattern of the second principal component (PC2) of 500-hPa geopotential height Z_{500} for four time periods: (a) March–May in the historical simulation, (b) June–August in the historical simulation, (c) March–May in the future high-emission (SSP585) simulation, and (d) June–August in the future SSP585 simulation. Each PC2 pattern was calculated over the NAD domain (same as magenta contours, Fig. 1c), and shading indicates the correlation between Z_{500} and the corresponding PC2 time series.

relationship, even results where the spring and summer correlations are comparable or nearly identical are noteworthy (e.g., GFDL-CM4).

The model FGOALS-I3-L provides a counter example to the overall tendency in CMIP6. It has one of the best four historical NAD patterns (blue bar in Fig. 4; $r = 0.74$), and this NAD pattern stays in summer under future warming (green bar, $r = 0.65$ – this is also the best-correlated future NAD pattern). The corresponding spatial patterns for model FGOALS-I3-L are mapped in Supplementary Fig. A.10. The model INM-CM4-8 is another interesting case; it has the best-correlated historical summer NAD, but correlation of its future PC2 pattern with NAD is relatively weak in spring and summer (bars in Fig. 4 and spatial patterns in Supplementary Fig. A.11).

4. Discussion and conclusion

Although previous studies acknowledge the effects of climate variability on irruption dynamics, they often focus on climate conditions during the year of irruption (direct effects) or at multi-year time lags (indirect effects) preceding the irruption as a proxy of mast-seeding dynamics (Koenig, 2001; Bateman et al., 2015). Our study expands on this research by linking irruptive migration in birds to the mechanistic pathway of climate variability and tree mast-seeding dynamics at a continental scale, enabling consideration of its future evolution under changing climate. We highlighted the importance of an alternating west-east dipole of mast seeding of conifer trees with opposite anomalies over western and eastern North America. The climate driver of this west-east mast seeding dipole, referred to as the North American Dipole, occurs during summer in the historical record, but shifts to spring in response to future climate warming during this century in most global climate models.

The climate system can respond in many ways to historical or future

warming. For example, there is robust evidence of historical changes in the seasonal cycle of atmospheric temperature since the pre-industrial era (Santer et al., 2018). Studies have predicted future changes in monsoons (Lee and Wang, 2014; Moon and Ha, 2020) and teleconnection mechanisms including the Pacific North American (PNA) pattern (Wang et al., 2022a), Madden-Julian Oscillation (MJO) (Cui and Li, 2019), and El Niño Southern Oscillation (ENSO) (Yeh et al., 2018; Watanabe et al., 2012), but in this study we find something different – a shift in the occurrence of a teleconnection to an earlier season under warming (here, the NAD shifts from summer to spring in 71 % of global climate models under the high greenhouse gas emission scenario). Temperature traces for these simulations indicate that future warming eliminates only about 2/3 of the $\sim 15^\circ\text{C}$ temperature difference between historical summer and future spring (Supplemental Fig. 7), meaning that this shift in circulation is not simply a future shift in the timing of temperatures characteristic of historical boreal summer. The result therefore suggests future warming-driven changes in timing or seasonal intensity of upstream drivers of the NAD, likely including Asian monsoonal convection and the MJO (Bui and Maloney, 2020; Wang and Wang, 2023; Dasgupta et al., 2020; Wang et al., 2022b).

Identification of this climate-masting-irruption mechanism and potential future changes in the timing of the climate driver have important implications for mast-seeding resource pulses in forest ecosystems. The response of mast-seeding dynamics to future predicted shifts in the NAD timing versus overall warming may depend on whether the timeframe of bud differentiation (into vegetative or reproductive buds) that is currently associated predominantly with summer temperatures (Krebs et al., 2012; LaMontagne et al., 2021) also shifts. If the NAD shifts to spring, but the timing of bud differentiation remains in summer, widespread synchrony in mast seeding patterns may result – eliminating the mast-seeding dipole; this would have consequences on the continental

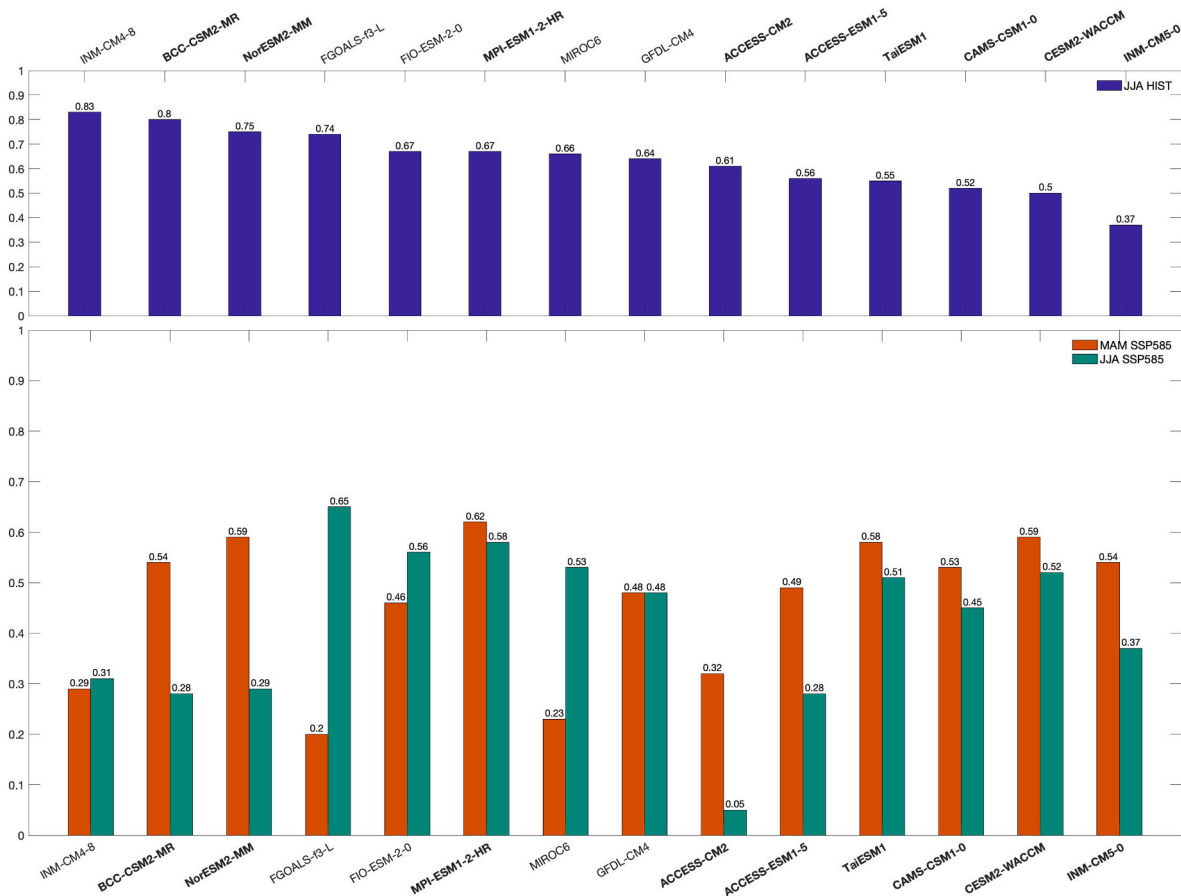


Fig. 4. Changes in the timing of the future NAD. For models participating in CMIP6, the bars indicate the spatial correlation between the observed historical summer North American Dipole (NAD) pattern and three simulated patterns: the model's historical summer PC2 pattern (blue bars), the models' future spring PC2 pattern (red bars), and the models' future summer PC2 pattern (green bars). The fourteen models selected have the highest spatial correlation between the simulated and observed NAD pattern (blue bars, all significant at $p < 0.01$). The future results correspond to a high-emission scenario referred to as SSP585 (Riahi et al., 2017). A bold model label indicates that this model's NAD pattern emerges in spring under future warming (i.e., its red bar is at least as large as its green bar).

dynamics of seed consumer populations. In addition, the delta-T hypothesis as a proximate driver of mast-seeding states that it is not absolute temperature that initiates abundant seed production, but greater positive differences between the summer temperatures during bud differentiation relative to the year prior to bud differentiation (Kelly et al., 2013). While this model explains how mast-seeding dynamics could be shielded from gradual warming effects, changes in climate variability could influence the frequency, magnitude, and, consequently, synchrony of mast-seeding (Kelly et al., 2013). If shifts in climate drivers such as NAD propagate shifts in masting, it will likely have ecosystem-scale consequences.

Many irruptive bird species demonstrate migratory plasticity that allows them to respond to prevailing environmental conditions (Stralberg et al., 2019). This high adaptive capacity could aid in tracking changes in resources, such as warming-driven shifts in mast-seeding timing or frequency. Irruptive boreal birds show evidence of changing irruption periodicity over time, demonstrating plasticity in annual movements (Widick et al., 2023). However, they also demonstrate poleward trends in southern irruption boundaries, indicating a long-term response in migration geography, potentially driven by changes in climate. Seasonal shifts in spatial and temporal resource dynamics could further alter migration patterns in space and time (Youngflesh et al., 2021), leading to changes in breeding phenology, survival, and, ultimately, reproductive success and population dynamics (Møller et al., 2008). Previous studies support this theory that climate-induced changes in resource phenology increase the vulnerability of migratory bird populations, driving changes in breeding phenology and population

trends (Møller et al., 2008). Additionally, climate variability influences demographic processes (Stenseth et al., 2002). While climate patterns such as ENSO and the North Atlantic Oscillation (NAO) can influence population dynamics broadly across taxa, the mechanisms underlying these responses to climate are poorly understood (Wan et al., 2022). Here we describe a mechanistic link between NAD, mast-seeding, and irruptive migration and uncover a projected shift in the climate driver under climate warming. Irruptions of boreal birds are part of a suite of continent-wide ecological phenomena linked to climate variability. Shifts in climate drivers such as NAD could lead to changes in the spatiotemporal patterns produced by ecological responses such as mast-seeding, which has cascading effects in ecosystems, influencing populations of seed consuming mammals and birds, and even influencing outbreaks of ticks and disease (Kelly et al., 2008; Anderson et al., 2011).

4.1. Data and materials availability

The FeederWatch bird count observations used in this project are available from the Cornell Lab of Ornithology (<https://www.birds.cornell.edu/home>). The mast-seeding datasets used for the study are available in the Dryad repository (Hackett-Pain et al., 2022). Reanalysis data sets including geopotential height, air temperature are available from the European Centre for Medium Range Weather Forecasts (<https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>). The precipitation data are available on the Global Precipitation Climatology Center at <https://climatedataguide.ucar.edu/climate-data/gpcc-global-precipitation-climatology-centre>. Coupled Model

Intercomparison Project phase6 (CMIP6) datasets are available at <https://esgf-node.llnl.gov/projects/cmip6/>.

CRedit authorship contribution statement

Husile Bai: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Courtenay Strong:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jalene M. LaMontagne:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Ivy V. Widick:** Writing – review & editing, Writing – original draft. **Benjamin Zuckerberg:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

Authors declare that they have no competing interests.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.174473>.

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