

Shifting avian spatial regimes in a changing climate

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In the present era of rapid global change, development of early warnings of ecological regime shifts is a major focus in ecology. Identifying and tracking shifts in spatial regimes is a new approach with potential to enhance understanding of ecological responses to global change. Here, we show strong directional non-stationarity of spatial regimes identified by avian community body mass data. We do this by tracking 46 years of avian spatial regime movement in the North American Great Plains. The northernmost spatial regime boundary moved >590 km northward, and the southernmost boundary moved >260 km northward. Tracking spatial regimes affords decadal planning horizons and moves beyond the predominately temporal early warnings of the past by providing spatiotemporally explicit detection of regime shifts in systems without fixed boundaries.

Ecological systems are complex and hierarchically organized in space and time¹, yet efforts to quantify ecological resilience and predict regime shifts have focused on the temporal dimension^{2,3}. This approach works well when the spatial boundaries of ecosystems are clear and fixed. For example, theoretical inference of early warning and pending regime change has advanced through studies of shallow lake ecosystems, which have hard boundaries that make it possible for scientists to ignore external spatial dimensions of these complex systems before regime shifts^{4,5}. Advancements have been made by extending early warning indicators such as autocorrelation into spatial contexts^{6–8}. However, the theory and methods still assume fixed spatial boundaries of regimes despite their being situated in open, complex and dynamic systems⁹.

The concept of spatial regimes represents a new frontier in resilience science that unifies both spatial and temporal dimensions into the study of regime persistence and change across ecosystems without fixed boundaries^{10,11}. Spatial regimes are defined as spatial extents with discrete boundaries at a given scale that exhibit relative homogeneity in structure and composition maintained by feedback mechanisms^{10,12}. Theory recognizes that all ecological regimes have geographic limits (spatial boundaries) but those limits may not be fixed or known¹². This perspective differs from classical investigations of resilience and regime shifts, which have focused primarily on systems with well-known boundary limits and where critical transitions have been observed over time^{2,13}. Many systems have porous boundaries (for example, grasslands and oceans), many taxa are highly mobile (for example, birds and pelagic fish), and system boundaries can shift rhythmically or in response to change drivers (for example, climatic and anthropogenic boundaries)¹⁴. There is no single appropriate scale to define spatial regimes in space or show how spatial regime boundaries move over time; this body of theory has only recently developed as more powerful metrics have emerged^{9,12}.

Here, we build on decades of ecological research on body mass size distributions^{15–17} to disentangle alternative scientific predictions about the behaviour of large-scale spatial regimes in an era of global environmental change. One prediction, on the basis of an extension of resilience theory, is that external environmental forcing will cause

idiosyncratic behaviour in spatial regimes undergoing collapse, similar to the responses of individual species before extinction^{18,19}. An alternative hypothesis is that spatial regimes are non-stationary and will be conserved because of strong positive feedbacks, such that spatial regime boundaries will move in a directional, orderly trajectory^{10,11}. Disentangling the predictable and orderly from the unpredictable and idiosyncratic provides the foundation for early warnings of critical transitions in nature⁹.

Results and discussion

We analysed 46 years of avian community body mass distribution data from the Great Plains of North America to identify spatial regime boundaries and then identified patterns in latitudinal spatial regime boundary movement over time. Analyses revealed regional, poleward shifts in both the southernmost and northernmost spatial regime boundaries. This supports our alternative hypothesis of conserved, directional and relatively ordered movement (Fig. 1). The northernmost regime boundary has moved faster: >590 km from 1970 baselines ($0.121 \pm 0.080^\circ$ latitude per year (13 km year^{-1}) at 90% confidence interval, CI) compared to about 260 km for the southernmost boundary ($0.053 \pm 0.051^\circ$ latitude per year (6 km year^{-1}) at 90% CI). These differential rates of spatial regime movement (northern versus southern boundaries; Fig. 1) match expectations associated with Arctic amplification and accelerated change in northern versus southern latitudes of temperate North America²⁰. Consistent with existing theoretical foundations²¹, the regime moving more quickly also carries with it greater interannual volatility in its location (Fig. 1).

Directional (northward) change in spatial regime boundaries occurred with relative stability in the number of spatial regimes identified over the past half-century (2.91 ± 0.39 , 90% CI; Fig. 2). The number of spatial regimes detected ranged from 0 to 5, with transitory regimes occurring periodically. Changing from the average of three spatial regimes, a fourth spatial regime emerged more consistently in the 2010s decade (2010–2015; Fig. 2). In the early decades of our study, spatial regime boundaries showed some congruence with the Great Plains biome's historic extent (Fig. 2). But in subsequent decades, spatial regimes expanded (southernmost

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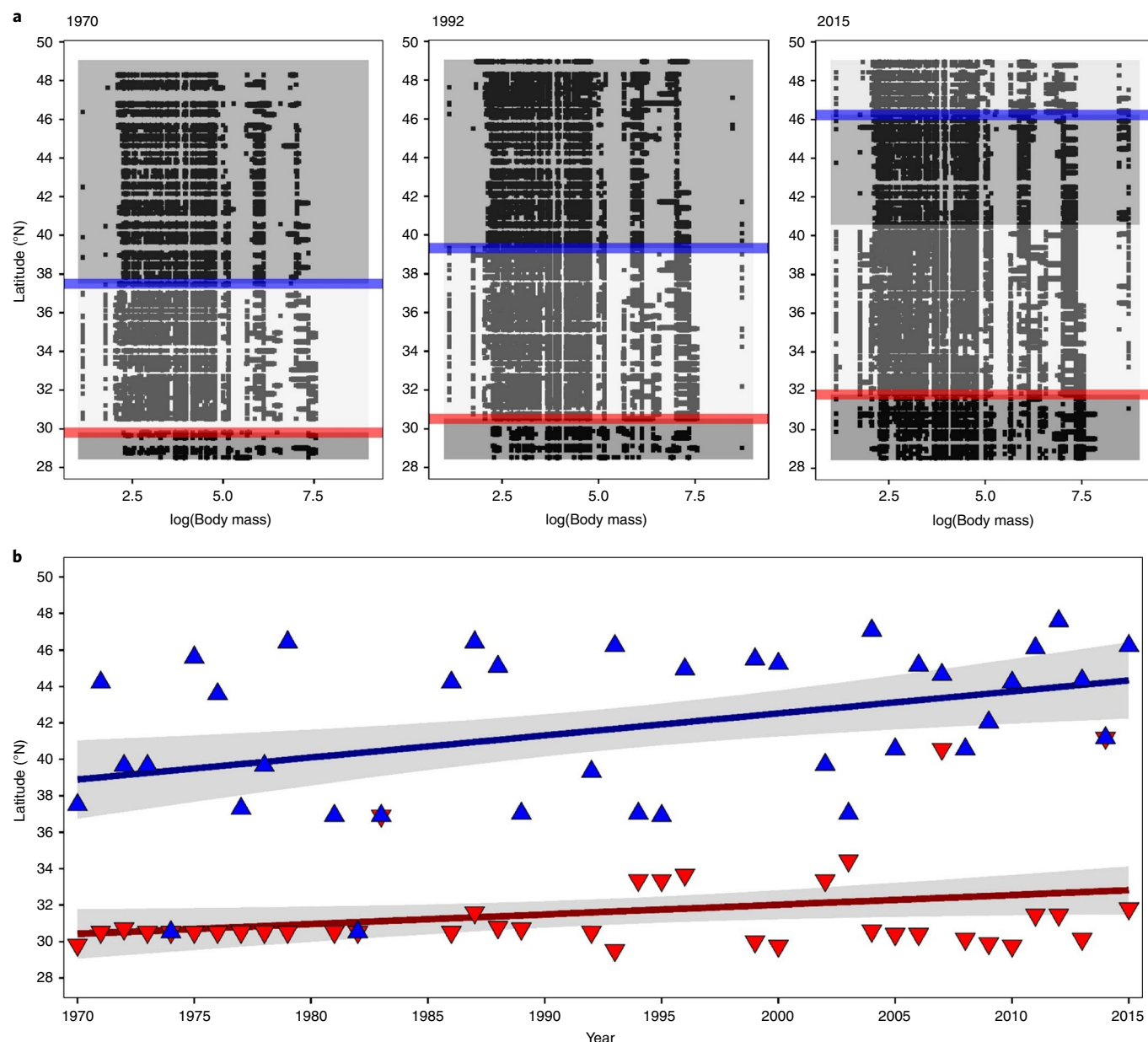


Fig. 1 | Shifts in spatial regime boundaries demonstrated by breeding bird body mass discontinuities from 1970 to 2015 in the North American Great Plains. a, Latitudinal spatial regime boundaries (y axis) determined by log-ranked avian body mass discontinuities (x axis). Black dots represent body mass aggregations identified using discontinuity analysis in each breeding bird survey route in the transect. Grey-scale boxes represent spatial regimes. The northernmost and southernmost spatial regime boundaries are highlighted by blue and red lines, respectively. **b**, Spatial regime boundaries (blue triangles, northernmost; red triangles, southernmost) detected each year. Lines represent modelled northernmost and southernmost spatial regime boundary movement over time with 90% CI (grey ribbon). When northernmost and southernmost boundaries were the same (that is, when only one spatial regime boundary was detected in a year), blue and red triangles overlap.

regime), moved northward (middle regime) and contracted (northern regimes), providing evidence that spatial regimes are rapidly reorganizing and diverging from historic biome extents by the 2010s (Fig. 2).

The cause of the northern movement is unknown but it is congruent with biogeographical patterns of change for multiple global change drivers in central North America. Climate change, anthropogenic pressures, wildfire trends and woody plant invasions have all operated along a putatively south-to-north trajectory over the past decades, particularly in the Great Plains^{22–27} (Fig. 3). Irrespective of mechanism, this finding suggests that spatial regimes, and the

animal body mass distributions we use to identify regimes, are conservative, as our alternative hypothesis predicts.

The addition of a spatial dimension without fixed boundaries to resilience quantification and regime shift detection allows for increased planning horizons in the face of global environmental change. We use the movement of spatial regime boundaries in the interior of central North America as an illustration (Fig. 4). For a network of protected lands in this region, advanced detection would come from tracking spatial regime boundaries in a surrounding window (Fig. 4). Knowing the ‘baseline’ boundary in 1970 and its average northward movement pattern, protected lands in the Flint

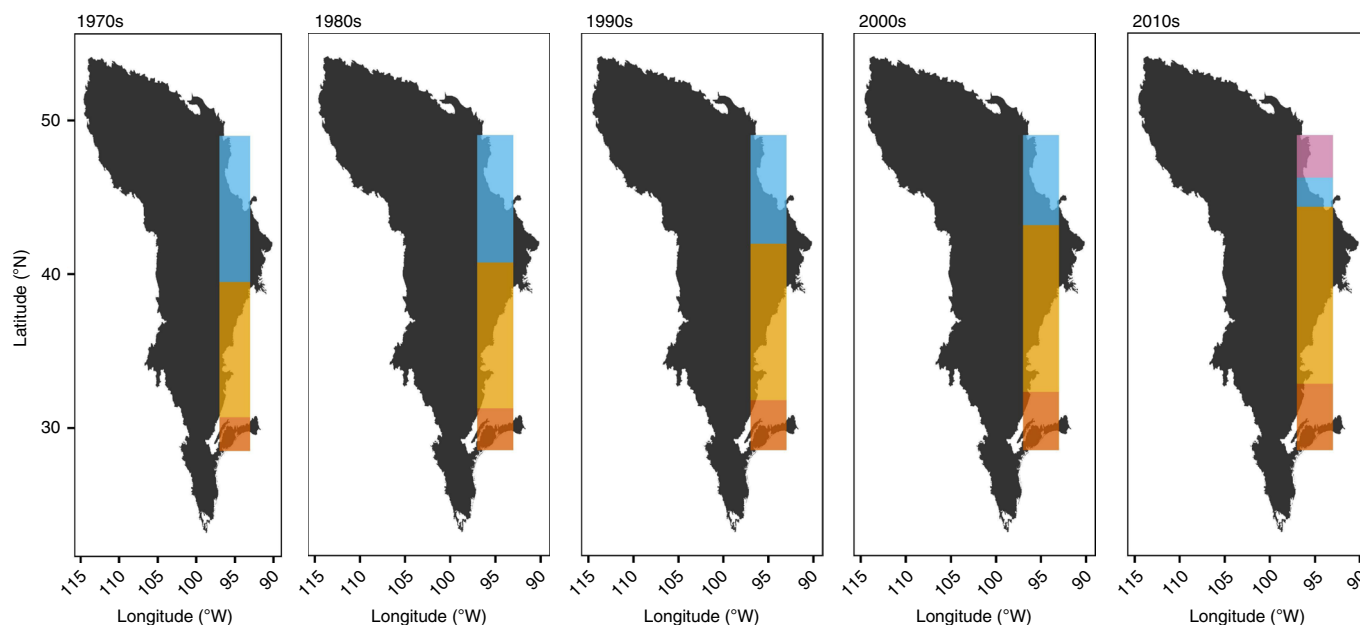


Fig. 2 | Visualization and tracking of predicted decadal spatial regimes and their boundaries in the North American Great Plains. Black polygons represent the historic Great Plains biome extent. Coloured bars represent the predicted extents of spatial regimes in the study area over five decades. The number of colours represent the average number of spatial regimes detected in each decade.

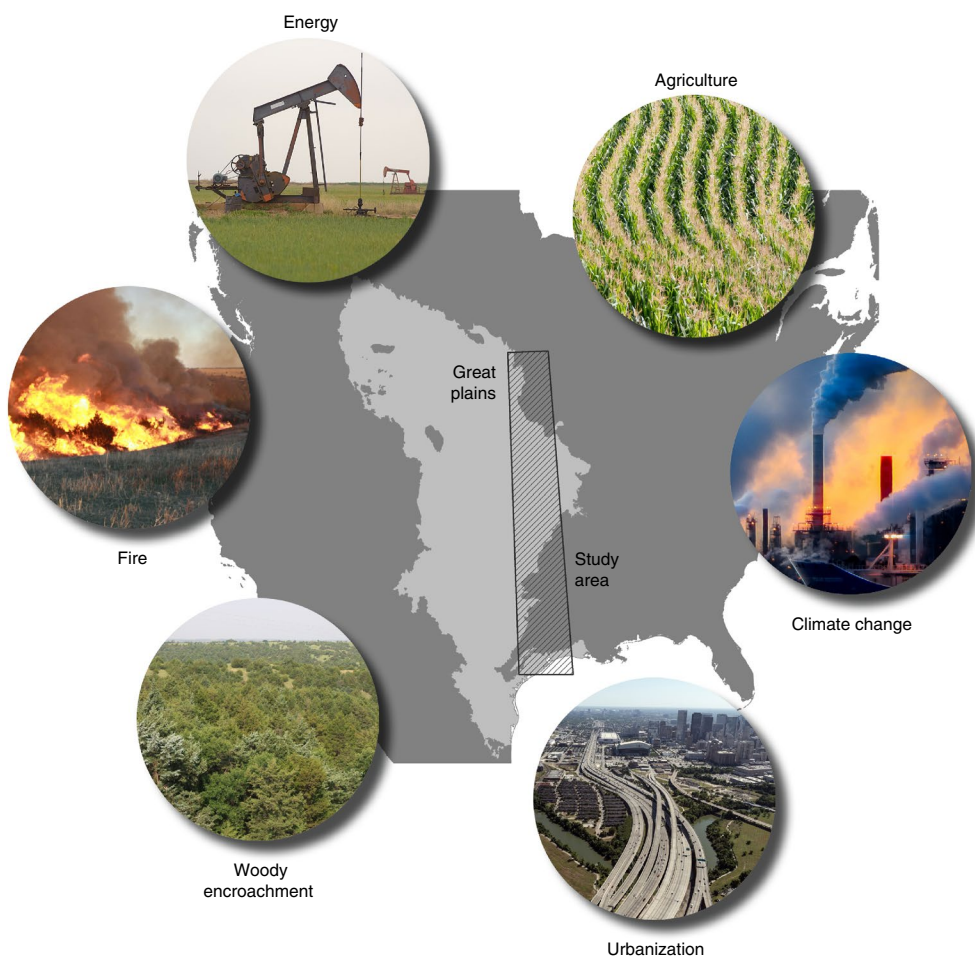


Fig. 3 | Global changes influencing ecological regimes in central North America. Global changes, such as agricultural land conversion, anthropogenic climate change, urbanization, woody plant encroachment, increasing frequency/intensities of fire and energy development, are all driving ecological change in the North American Great Plains in a putatively south–north trajectory. Predictable, directional (poleward) movement of spatial regime boundaries in the Great Plains corresponds to the trajectories of global change drivers. Credit: USDA, NRCS Texas (agriculture).

Hills ecoregion had decades of early warning that the entire ecoregion would soon experience an imminent transition; protected lands in the Western Corn Belt Plains ecoregion had >40 year of advanced warning (Fig. 4). In this example, a spatial regime boundary moving closer to a given location warns of an impending abrupt change—but a change that is relatively predictable as one regime replaces another. Theoretically, this should precede traditional generic signals of early warning of a regime shift^{28–30}. Traditional early warning signals, such as critical slowing down, rising variance and flickering, rely on ecological data departing and returning to a baseline; this essentially requires a temporal lag before detecting even a single iteration of a signal^{6,29–31}.

Our analysis suggests that it is now possible for the science of early warning to foster earlier adaptation in environmental management at subcontinental scales, forcing increased awareness of the challenges inherent in the management of stationary ecological conditions at a given location³². As a moving ecological regime approaches or passes a given location, it becomes increasingly likely that the existing ecological regime will collapse and a location managed to reflect earlier regimes will become a ‘ghost of regimes past’. Policies that mandate management for ghosts of regimes past, regardless of the surrounding regime, may be setting themselves up for failure in an era of global change and uncertainty^{33,34}. Acknowledging this reality has been difficult for ecosystem managers at a given location to accept. Laws such as the Endangered Species Act in the United States currently lack the flexibility necessary to solve this general problem of managing for ghosts of past regimes because single species are often the prime conservation targets. To illustrate this: in our example of spatial regime boundaries shifting northward past a conservation land in central North America (Fig. 4), land managers tasked with preserving historical plant–animal associations will continue to burn and mechanically remove woody plants to maintain remnants of the historic tallgrass prairie regime while simultaneously losing ground to encroaching woody regimes due to positive feedbacks (for example, propagule pressure and avian seed dispersal)^{27,34}. Once these coercive management efforts wane, positive feedbacks will quickly shift to the basin of attraction of the surrounding spatial regime^{12,35}. An alternative approach for land managers is to embrace northward-moving spatial regimes and align conservation efforts in northern protected areas congruent with the needs of species from a formerly southern area; and to ensure viable, dynamic corridors where and when needed.

Spatial regimes may not follow global change trajectories when strong local drivers exist, such as immobile environmental filters (for example, sandy soil substrates and alkaline soils) or anthropogenic or geographic barriers. In these cases, theory predicts that spatial regimes will contract and not ‘move through’ these barriers^{36,37}. Over time, if global drivers outweigh local drivers, spatial regime boundaries may show high variance as the local system collapses and reorganizes in the same location. For example, in our study, the southernmost spatial regime boundary (Fig. 2) corresponds broadly with the coastal prairie, which is associated with unique sandy soil types and has experienced major landscape fragmentation and conversion through urbanization and energy development^{22–27} (Fig. 3). The southernmost spatial regime boundary showed fidelity to the geographic boundary of the coastal prairie from 1970 to 1993 (Fig. 1). In the mid-1990s, the southernmost boundary began to vary more widely in latitude between its original location and nearly the latitude of the historic northernmost boundary (Figs. 1 and 2).

Management of spatial regimes, given their conservative nature and tools to identify their boundaries, should encourage more adaptive measures that both: (1) consider the current and potential future scale of change associated with underlying driving processes and (2) embrace ecological non-stationarity as part of short-term and long-term planning horizons. Specializations in conservation ecology

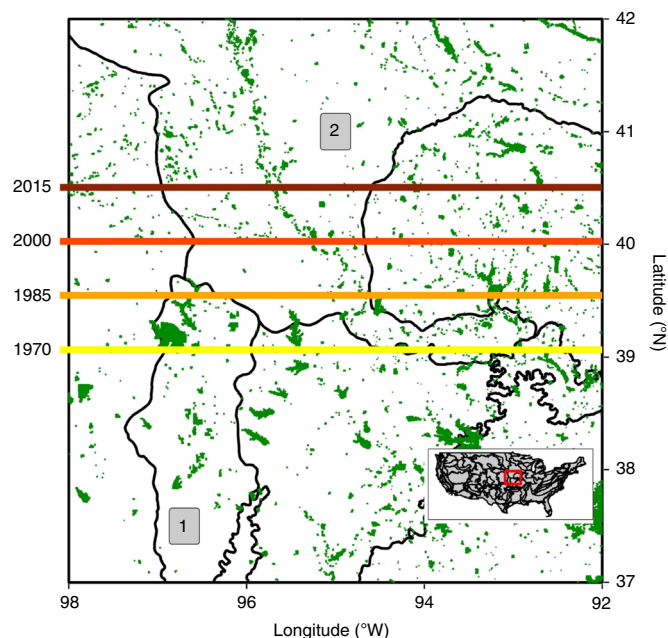


Fig. 4 | Spatial regime boundary movement between 37 and 42° latitude across a network of protected areas in central North America. Black lines indicate level III US Environmental Protection Agency ecoregion boundaries; green polygons indicate protected areas. The ecoregion labelled ‘1’ is the Flint Hills ecoregion; the ecoregion labeled ‘2’ is the Western Corn Belt Plains ecoregion. Predicted spatial regime boundaries (coloured horizontal lines) correspond with linear predictions for the years 1970, 1985, 2000 and 2015 ($\beta = 0.032 \pm 0.026^\circ$ latitude per year; 90% CI; $F = 4.093$; $P = 0.052$).

have struggled to fully move away from the legacy of equilibrium management, despite many resilience-based management frameworks^{34,38,39}. We see the addition of spatial dimensionality without fixed boundaries to resilience quantification and early warning detection, particularly how spatial regimes behave over time, as a necessary ingredient for modernizing environmental management in the Anthropocene. Spatial monitoring of regime change over time could further efforts to create collaborative networks among land stewards and more strategically develop protected areas acknowledging the strong non-stationarity that currently exists^{10,12,40}. Instead of focusing on historic species assemblages and their idealized distribution envelopes, a successful network would focus on system-level maintenance of resilient, desirable regimes in the face of change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at <https://doi.org/10.1038/s41558-019-0517-6>.

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Author contributions

C.P.R. contributed to conceptualization, programming, validation, formal analysis, data curation, all writing aspects, visualization and project administration. C.R.A., D.G.A. and D.T. contributed to funding acquisition, conceptualization, all writing aspects and visualization.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Experimental design. Breeding Bird Survey data manipulation. We used 46 years (1970–2015) of the US Geological Survey's North American Breeding Bird Survey data, which is a freely available dataset of avian community composition collected by trained observers along permanent, geo-referenced roadside routes across the North American continent⁴¹. Because routes were still being established in the initial years of the Breeding Bird Survey, especially in the Great Plains and western portions of North America, to avoid biased estimates of presence/absence we consider route data starting in 1970, when about 50% of currently active routes had been established (Supplementary Table 1). Along each around 39.5-km route, observers make 50 stops (once every 0.8 km) and conduct point-count surveys at each stop. During a point-count survey, observers stand at the stop and record the abundance of any bird species they detect visually or aurally in a 0.402-km radius for 3 min. Surveys begin 30 min before local sunrise and last until the whole route is completed. To increase uniformity in bird detection probability, observers conduct surveys only on days with low wind speeds, high visibility and little (or no) rain. Routes are distributed relatively evenly throughout the United States. Due to latitudinal differences in breeding season timing, routes may begin as early as May or as late as July.

Because of known negative observation biases for waterfowl and allied families, and because water-dwelling avian families follow different body mass patterns compared with terrestrial avian families, we removed all species from the Anseriformes, Gaviiformes, Gruiformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes and Suliformes families from the analysis^{16,41}. We also removed hybrids and unknowns; and we condensed subspecies to their respective species.

Belt transect. Multiple global change drivers are exerting influence in a south-to-north pattern in the Great Plains. For instance: climate change is shifting native and agricultural plant phenologies⁴² and geographic centres of plant species distributions⁴³; woody plant encroachment is causing regime shifts from historically grassland regimes to woodland or shrubland regimes^{37,38}; fire frequency and size has increased by >400% in the Great Plains²⁶; energy development such as oil and gas extraction reduced net primary productivity by about 4.5 Tg between 2000 and 2015 (ref. 25); agricultural land conversion has led to the northern plains losing much of its remaining grassland after commodity prices surged at the beginning of the 21st century⁴⁴; and urbanization and population growth in the Great Plains has continually increased in and around already populated areas²². To capture latitudinal spatial regime movement that may be responding to these south-to-north global change drivers, we selected a belt transect on the ecotone of the Great Plains and Eastern Temperate Forests extending from the Gulf of Mexico to the edge of the boreal forest in Canada. Specifically, the belt transect extended south–north from 28–49° latitude (about 2,300 km) and east–west from 93–97° longitude (about 350 km).

Statistical analysis. Identifying discontinuities. For each route falling in the belt transect, we identified discontinuities in avian community body masses by rank-ordering the log-transformed body masses of each species observed at each route for each year. We obtained mean body mass estimates for all species in the analysis from the *CRC Handbook of Avian Body Masses*⁴⁵. We then used the 'discontinuity detector' method⁴⁶ on the log-ranked body masses, which is on the basis of the Gap Rarity Index for detecting discontinuities in continuous data⁴⁷. For taxa with determinant growth, mean body mass has been shown to reliably differentiate size aggregations and is strongly allometric to the scales at which functions are carried out by organisms^{48,49}. Because the discontinuity detector method is known to overestimate discontinuities in observations with low species richness, we removed any routes with <40 species observed in a given year (Supplementary Table 1). We used a power table⁵⁰ to account for sample size (the number of species observed at each Breeding Bird Survey route in a given year) and average variance in body masses⁴⁵ to adjust the critical *d*-value (the value on the basis of Monte Carlo simulations that identifies significant discontinuities) where *N* varied⁵¹ (Supplementary Table 2).

Spatial regime detection. To detect spatial regimes in each year, we ordered routes in ascending latitude and transformed the discontinuities into a data matrix for analysis. Specifically, in order from the lowest ranked body mass aggregation to the highest, we calculated the sizes of body mass aggregations (the log-ranked length of each aggregation), the sizes of gaps between aggregations (the log-ranked length of each gap) and the locations of aggregations (the log-transformed body mass of the species with the lowest body mass in each aggregation) for each route¹⁷. We cast these into a matrix using the 'dcast' function in the 'reshape2' and 'data.table' packages in R, where every row represented a route in a given year and every column an aggregation size, gap size or aggregation location^{52–54}. We calculated separate Bray–Curtis dissimilarity matrices from each year's data.

To identify spatial regimes, we ran constrained hierarchical clustering on each year's distance matrix starting at the southernmost (lowest latitude) Breeding Bird Survey route and proceeding by order of latitude to the northernmost Breeding Bird Survey route (highest latitude). Constrained hierarchical clustering directionally separates multivariate data series into homogeneous, non-overlapping

segments; it constrains clusters so that only adjacent, contiguous samples (a contiguous segment of Breeding Bird Survey routes along a spatial transect) are allowed to cluster^{17,55}. This method is commonly used to delineate temporally ordered regimes in paleo community data^{56,57} and to detect significant community transitions along spatial transects^{55,58}. To perform constrained hierarchical clustering, we used the 'chclust' function with the 'CONISS' method from the 'rioja' package in R (ref. 39).

We used the broken stick model ('bstick.chclust' from the 'rioja' package in R) to determine the number of significant clusters^{17,59,60}. The broken stick method, commonly used in conjunction with constrained hierarchical clustering, tests the distribution of clusters from constrained hierarchical clustering against multiple null random distributions of clusters to ascertain the number of significant clusters^{17,57,60}. Because constrained hierarchical clustering identifies homogeneous, non-overlapping areas of self-similarity, significant clusters can be interpreted as regimes; boundaries between significant clusters can be interpreted as regime boundaries. Therefore, we considered the latitudes of significant cluster boundaries from each year to be the location of spatial regime boundaries from that year¹⁷.

Tracking movement in spatial regimes. We tested for non-random movement in spatial regime boundaries over time by fitting generalized additive models ('mgcv' package in R) to the northernmost and southernmost spatial regime boundaries⁶¹. Because generalizing additive models did not detect non-linearity in either the northernmost (estimated degrees of freedom (edf) = 1.00, *F* = 6.56, *P* = 0.02) or southernmost (edf = 1.00, *F* = 3.21, *P* = 0.08) spatial regime boundaries, we estimated the mean rate of movement in spatial regime boundaries using linear regression (Fig. 1). We classified the northernmost boundary each year as the spatial regime boundary with the greatest latitude; we classified the southernmost boundary each year as the spatial regime boundary with the lowest latitude. We excluded years from the linear regression analysis in which we detected no spatial regimes from the analysis (1980, 1984, 1985, 1990, 1991, 1997, 1998 and 2001). For years in which only one spatial regime boundary was detected (years with only two spatial regimes), the single boundary was counted as both the northernmost and southernmost boundary.

We also assessed spatial regime boundary movement at the scale of a regional protected areas network. Specifically, we tracked spatial regime boundary movement from 1970 to 2015 between 37 and 42° latitude to assess the utility of spatial regime tracking for early warnings for land management and the length of planning horizons spatial regimes provided (Fig. 4). As above, we quantified spatial regime boundary latitudinal movement over time using linear regression.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data are available in the Supplementary Data.

Code availability

R code and instructions for repeating analyses are available in the Supplementary Data.

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Reporting Summary

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Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

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- ☐ ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
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- ☐ ☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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- ☐ ☒ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated
- ☐ ☒ Clearly defined error bars
State explicitly what error bars represent (e.g. SD, SE, CI)

Our web collection on [statistics for biologists](#) may be useful.

Software and code

Policy information about [availability of computer code](#)

Data collection

We used the publicly available North American Breeding Bird Survey dataset maintained by the US Geological Survey.

Data analysis

We used R version 3.5.0 for all analyses. We have attached reproducible computer code for R statistical software, and we have reported sources for functions and code not available via CRAN packages.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

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- Accession codes, unique identifiers, or web links for publicly available datasets
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All data is freely available via the U.S. Geological Survey's North American Breeding Bird Survey database. We have also included the body mass and species presence/absence data used in a supplementary file along with reproducible computer code.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used North American Breeding Bird Survey data (BBS) along a south-to-north belt transect extending south-north from 28 – 49 degrees latitude (approximately 2300 km) and east-west from 93 – 97 degrees longitude (approximately 350 km). We then identified spatial boundaries in bird regimes (spatial regimes) and tracked their movement over time.
Research sample	We collected 46 years (1970 – 2015) of the U.S. Geological Survey's North American Breeding Bird Survey data (BBS), which is a freely available dataset of avian community composition collected by trained observers along permanent, georeferenced roadside routes across the North American continent. Because routes were still being established in the initial years of the BBS, especially in the Great Plains and western portions of North America, to avoid biased estimates of presence/absence we consider route data starting in 1970, when approximately 50% of currently active routes had been established (Table S1). Along each approximately 39.5 km route, observers make 50 stops (once every 0.8 km) and conduct point-count surveys at each stop. During a point-count survey, observers stand at the stop and record the abundance of any bird species they detect visually or aurally within a 0.402 km radius for three minutes. Surveys begin thirty minutes prior to local sunrise and last until the whole route is completed. To increase uniformity in bird detection probability, observers conduct surveys only on days with low wind speeds, high visibility, and little or no rain. Routes are distributed relatively evenly throughout the United States. Due to latitudinal differences in breeding season timing, routes may begin as early as May or as late as July.
Sampling strategy	Our sample size was simply the number of North American Breeding Bird Survey routes conducted each year within our study area. We established the belt transect due to the multiple global change drivers (e.g., climate change) influencing ecological regimes along the ecotone of the Great Plains and Eastern Temperate Forests extending from the Gulf of Mexico to the edge of the boreal forest in Canada.
Data collection	The North American Breeding Bird Survey conducts annual roadside avian point-count surveys. These surveys are conducted by volunteers and compiled in a central database maintained by the US Geological Survey.
Timing and spatial scale	We analyzed data from the North American Breeding Bird Survey from 1970 - 2015. Data is collected annually. We considered all breeding bird data extending south-north from 28 – 49 degrees latitude (approximately 2300 km) and east-west from 93 – 97 degrees longitude (approximately 350 km).
Data exclusions	Because the discontinuity analysis method we used became biased at low species richness, we excluded breeding bird survey routes on which < 30 bird species were detected. This is an established cutoff in the literature--see our citations for reference. Additionally, because of known negative observation biases for waterfowl and allied families and because water-dwelling avian families follow different body mass patterns than terrestrial avian families, we removed all species from the Anseriformes, Gaviiformes, Gruiformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes, and Suliformes families from the analysis. We also removed hybrids and unknowns, and we condensed subspecies to their respective species.
Reproducibility	Because the number of survey routes varied across years, we initially checked our results by only using survey routes that were established in the beginning of the study (1970) and were repeated every year after. Although this resulted in a lower sample size, we found results (spatial regime movement patterns) were extremely similar to when we used the entire dataset.
Randomization	Because our analysis determined the groups we analyzed (i.e., spatial regime boundaries), randomization was not required.
Blinding	Because our data was collected from a publicly-available database, we did not use blinding.
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging