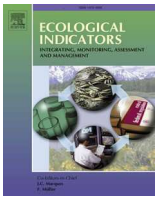
Ecological Indicators 136 (2022) 108567

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Tracking spatial regimes in animal communities: Implications for resilience-based management

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ARTICLE INFO

Keywords:
Alternative states
Bird
Boundary detection
Early warning
Grassland
Regime shift
Spatial resilience
Wombling
Woody plant encroachment

ABSTRACT

Spatial regimes (the spatial extents of ecological states) exhibit strong spatiotemporal order as they expand or contract in response to retreating or encroaching adjacent spatial regimes (e.g., woody plant invasion of grasslands) and human management (e.g., fire treatments). New methods enable tracking spatial regime boundaries via vegetation landcover data, and this approach is being used for strategic management across biomes. A clear advancement would be incorporating animal community data to track spatial regime boundaries alongside vegetation data. In a 41,170-hectare grassland experiencing woody plant encroachment, we test the utility of using animal community data to track spatial regimes via two hypotheses. (H1) Spatial regime boundaries identified via independent vegetation and animal datasets will exhibit spatial synchrony; specifically, grassland:woodland bird community boundaries will synchronize with grass:woody vegetation boundaries. (H2) Negative feedbacks will stabilize spatial regimes identified via animal data; specifically, frequent fire treatments will stabilize grassland bird community boundaries. We used 26 years of bird community and vegetation data alongside 32 years of fire history data. We identified spatial regime boundaries with bird community data via a wombling approach. We identified spatial regime boundaries with vegetation data by calculating spatial covariance between remotely-sensed grass and woody plant cover per pixel. For fire history data, we calculated the cumulative number of fires per pixel. Setting bird boundary strength (wombling R^2 values) as the response variable, we tested our hypotheses with a hierarchical generalized additive model (HGAM). Both hypotheses were supported: animal boundaries synchronized with vegetation boundaries in space and time, and grassland bird communities stabilized as fire frequency increased (HGAM explained 38% of deviance). We can now track spatial regimes via animal community data pixel-by-pixel and year-by-year. Alongside vegetation boundary tracking, tracking animal community boundaries can inform the scale of management necessary to maintain animal communities endemic to desirable ecological states. Our approach will be especially useful for conserving animal communities requiring large-scale, unfragmented landscapes—like grasslands and steppes.

1. Introduction

Spatial regime monitoring has strong potential to advance resilience-based management (Allen et al., 2016; Garmestani et al., 2020). Derived from resilience theory, spatial regimes are defined as the spatial extent and statistically delineated boundaries of an ecological state (Sundstrom et al., 2017). Spatial regimes exhibit strong spatiotemporal order as they move, expand, contract, appear, and disappear in response to disturbances (Roberts et al., 2022), global change (Iknayan and Beissinger 2020), and human management (Bestelmeyer et al. 2011). Using high resolution vegetation data, recent studies showcase how tracking boundaries between ecological states (i.e., tracking spatial regimes) can

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https://doi.org/10.1016/j.ecolind.2022.108567
Received 7 October 2021; Received in revised form 3 December 2021; Accepted 11 January 2022
Available online 29 January 2022

quantify outcomes of local-scale management actions such as grassland restoration via brush management and prescribed fire (Uden et al. 2019) and provide spatially-explicit early warnings of spatial regime shifts in the form of contracting desirable regime extents or expansion of undesirable regimes (Roberts et al., 2021). Building from this work, the "tracking spatial regimes approach" defines management successes as spatial expansion or stabilization of desirable vegetation regimes. Conversely, it defines management failures and early warnings of eroding resilience as an undesirable vegetation regime displacing a desirable vegetation regime in space. Using this framework, tracking spatial regimes via vegetation has been adopted by a biome-scale conservation framework to conserve grassland regimes in the face of woody plant encroachment (NUSDA NRCS, 2021). It is also being used to craft regional strategies for conserving sagebrush ecosystems and combating shifts to exotic annual grass-dominated regimes (USDA NRCS, 2020).

A clear next step in advancing the approach is to track spatial regime boundaries via animal community data. Using animal community data alongside vegetation data to track spatial regimes would extend the definition of successful management to expansion or stabilization of boundaries of desirable vegetation and desirable animal regimes. Using multiple, independent lines of evidence to track spatial regimes (vegetation and animal communities) will increase inferential power to quantify management outcomes for multiple ecosystem services, such as restoring rangeland productivity and animal biodiversity (Timmer et al., 2021). Recent studies have shown spatial regime boundaries can be tracked using animal data at broad scales. For example, sub-continental avian regime boundaries moved $>$ 500 km poleward in a tractable fashion, ostensibly in response to climate change and woody plant encroachment (Roberts et al., 2019), and spatial regime shifts have been documented in coastal fish communities (Eklöf et al., 2020). However, this pursuit is complicated by two factors: animals' high mobility and the typically coarser spatial resolution of animal monitoring data relative to remotely-sensed vegetation data. Respectively, these factors could muddle boundary signals or make them too coarse to be comparable to vegetation boundaries at all but the broadest scales.

The key to incorporating animal community data into the tracking spatial regimes approach is devising a workflow that produces outputs that 1) are comparable to current vegetation applications in terms of spatiotemporal resolution and 2) demonstrably respond to land management. A simple and theory-grounded way to test for these requisites is to test for spatiotemporal synchrony between vegetation boundaries, land management history, and animal community boundaries (Wang et al., 2019). There is some evidence for synchrony across taxa in space and time (Johnson and Hering 2010). There is also some support for spatial synchrony between vegetation and animal boundaries (Kent et al. 2013; Andersen and Steidl, 2019; Roberts et al., 2022) and between land management and animal boundaries (Severson et al., 2017; Olsen et al., 2021). But it is uncertain if spatial synchrony will manifest with sufficient strength or clarity to make tracking boundaries in animal communities useful for incorporating into the tracking spatial regimes approach.

An ideal system to test for synchrony between vegetation and animal boundaries is a grassland experiencing woody plant encroachment. Woody plant encroachment is a spatially contagious regime shift (Bestelmeyer et al., 2011; Ratajczak et al., 2014; Donovan et al., 2018), making it ideal for applying the tracking spatial regimes approach. It is also a globally relevant conservation challenge: on multiple continents, woody plant encroachment is leading to regime shifts from grasslands to woodlands, reducing aquifer recharge, disrupting rural livestock-based economies, increasing wildfire risk, and causing precipitous declines in grassland animal biodiversity (Veldman et al., 2015; Archer et al., 2017; Adane et al., 2018; Donovan et al., 2020). Importantly, grassland animal communities—particularly grassland birds—are known to decline under even minimal or distant woody plant encroachment (Cunningham and Johnson, 2006; Thompson et al., 2014; Fuhlendorf et al., 2017). Due to this high sensitivity to woody plant encroachment, boundaries between grassland and woodland bird communities should manifest with sufficient strength and clarity to correspond with vegetation regime boundaries and land management (i.e., grassland restoration actions such as fire treatments; Cunningham and Johnson, 2019).

Here, our goal is to test the utility of a workflow for tracking spatial regimes via animal community data. We set our study in a protected area within the North American Great Plains that is actively managed via fire to maintain tallgrass prairie in the face of regime shifts resulting from biome- and local-scale woody plant encroachment. We test two hypotheses. (H1) Spatial regime boundaries identified via independent vegetation and animal datasets will synchronize in space and time. Specifically, we expect animal community boundary strength to peak at weak-moderate vegetation boundary strengths, and we also expect animal community boundary strength will decline at strong vegetation boundaries because bird communities will shift from grassland to woodland communities due to grassland birds' sensitivity to even minimal woody plant cover (Thompson et al., 2014; Roberts et al., 2021). (H2) Because fire is a critical negative feedback for maintaining the grassland regime that historically dominated our study area (Twidwell et al., 2020), animal community boundary strength should decline as fire frequency increases.

2. Methods

2.1. Study site

We conducted this study at Fort Riley Army Base, Kansas, USA. Fort Riley is a military reservation encompassing approximately 41,170 ha and lies in the Flint Hills ecoregion of the North American Great Plains. Elevation ranges between 335 and 397 m. Two major alternative regimes dominate Fort Riley: a grass-dominated regime and a woody plant-dominated regime (Ratajczak et al., 2014; S. Stratton, Fort Riley DPW Environmental Division, oral comm, 2018). There is no livestock grazing in Fort Riley, and the only large herbivores are white-tailed deer (*Odocoileus virginianus*) and a small, reintroduced population of elk (*Cervus canadensis*). Historically, the grassland regime dominated the base—especially in the north-northwest—and a woody plant regime dominated a small portion in the southeast along the Kansas River (S. Stratton, Fort Riley DPW Environmental Division, oral comm, 2018). The US Department of Defense values grasslands for training purposes, and many grassland bird species are listed as species of greatest conservation need in the Flint Hills (Rohweder, 2015). Thus, for land managers at Fort Riley, preventing woody spatial regimes from displacing grass spatial regimes in the north-northwest portion of Fort Riley would be considered a management success, whereas woody regimes displacing grass regimes would be a management failure. To maintain the grassland regime in the north-northwest of the base, land managers at Fort Riley implement relatively frequent and large fire treatments, and random fire ignitions from military training also contribute to maintaining grasslands (S. Stratton, Fort Riley DPW Environmental Division, oral comm, 2018). Nevertheless, due to fire suppression, human tree planting, increased atmospheric carbon dioxide, and positive feedbacks such as woodland birds dispersing tree seeds, woody plant regimes are actively displacing grassland regimes within and around Fort Riley (Archer et al., 2017; Roberts et al., 2018; Roberts et al., 2022). Importantly, we excluded a roughly circular area in the east-central of Forty Riley from analyses because biologists were not able to conduct bird surveys there due to intensive military exercises and munitions firing (Fig. S1).

2.2. Data collection

2.2.1. Bird community data

Using a stratified random design based on soil-land cover type combinations, Fort Riley personnel established 59 bird community sampling locations in 1991 (Fig. S1). Fort Riley personnel surveyed

sampling locations annually 1991–2017 during the breeding season (May - June). At each sampling location, surveyors quantified bird community composition along a 100 m transect. Transects originated at the sampling location and extended 100 m along a randomly chosen azimuth used for all years. Surveyors walked from the start to the end of the transect in 6 min, stopped for 8 min at the end of the transect, and then walked from the end to the start of the transect for 6 min. Surveyors recorded the number and species of all birds seen or heard during these surveys.

2.2.2. Vegetation data

We used the Rangeland Analysis Platform's continuous 900 m^2 (30 × 30-meter pixels) annual percent cover data of plant functional groups, version 2 (Jones et al., 2018; Allred et al., 2021). We specifically used tree (2.8% mean absolute error) and perennial herbaceous forbs/grass cover (10.3% mean absolute error) estimates (Allred et al., 2021). For simplicity and because forbs comprised a smaller portion of vegetation communities, we hereafter refer to "perennial herbaceous forbs/grasses" as "grasses". Due to error in vegetation cover estimates generated by urbanized areas (roads, buildings), water (lakes, ponds, streams, rivers), and croplands, we used the 2016 National Land Cover Database to mask pixels falling into these categories (Homer et al., 2015; Allred et al., 2021).

2.2.3. Fire history data

We obtained fire history data from the Monitoring Trends in Burn Severity dataset (MTBS; Eidenshink et al., 2007). MTBS recorded 66 fires within the Fort Riley Army Base property from 1984 (the beginning of MTBS data) to 2016 (the year before the final year of this study). Because MTBS only records fires > 400 ha in the western United States, we acknowledge that this is not an exhaustive fire history dataset. However, this minimum MTBS fire size matches the typical sizes of prescribed fires at Fort Riley (S. Stratton, Fort Riley DPW Environmental Division, oral comm, 2018), and it is some of the best data currently available. We downloaded fire history data as polygon shapefiles that contained ignition date information. We then converted polygons into three 900 m^2-resolution rasters (30 × 30-meter pixels), where each raster pixel value indicated the cumulative number of fires that occurred in each pixel from 1984 to 1991, 1984–2005, and 1984–2016. We assumed pixels with no recorded fires experienced no fire between 1984 and 2016 and set their values as 0.

2.3. Identifying boundaries in bird communities and vegetation

Using the data described above, we developed and implemented a multi-step workflow to identify spatial regime boundaries using bird community data (Fig. 1) and vegetation data. This workflow—described below—generated two raster datasets which were then used alongside fire history data to test our two hypotheses.

2.3.1. Identifying bird community boundaries

We identified bird community spatial regime boundaries using geographically weighted regression as a generalized wombling method for point-based data (hereafter "wombling"; Diniz-Filho et al., 2016). Wombling is an established approach for identifying boundaries between ecological entities (Womble, 1951), and it has been performed via various methods (Barbujani et al., 1989; Fitzpatrick et al., 2010; Kent et al., 2013). The geographically weighted regression method for wombling takes geographic coordinates and an environmental variable, such as ordination values, and produces linear regression statistics (e.g., R^2 values) for each sampling location (Diniz-Filho et al., 2016). Higher R^2 values indicate boundaries (locations of abrupt environmental change), and low R^2 values indicate core areas (locations of relative homogeneity and similarity) of spatial regimes.

Here, we used multivariate bird community sampling data and locations as inputs for the wombling method. Before performing ordination, we used a Hellinger transformation to correct for rare species (Dray et al., 2012). We then performed principal components analysis (PCA) on the full transformed dataset (all years, all sampling locations). We used the first axis of the PCA as the biotic ("environmental") values for each point, and we used the latitude and longitude of each point as the geographic coordinates (Diniz-Filho et al., 2016). We ran wombling on each year of our data (1991–2017), except 2016 because < 30% of bird point count locations were surveyed that year.

To transform wombling outputs into a form comparable to vegetation boundaries and fire history data, we used a generalized additive model (GAM) to predict wombling values in space and time. For the GAM's response variable, we used wombling R^2 values for all sampling locations/years. For the predictor variable, we used a smoothed three-way interaction term of time (year) and space (easting and northing in Universal Transverse Mercator plane coordinate grid system). We then used the GAM outputs to predict wombling values across the extent of the study area as continuous raster surfaces at 900 m^2 spatial resolution (to match vegetation remote-sensing resolution—see below) for three years representing the beginning (1991), middle (2005), and end (2017) of the study. Because wombling R^2 values can only range from 0 to 1, we truncated GAM predictions < 0 (3% of predicted values) to be 0 and GAM predictions > 1 to be 1 (0.2% of predicted values). Hereafter, we refer to these predicted wombling R^2 values as "GAM-predicted wombling R^2 values."

2.3.2. Identifying vegetation boundaries

We identified grass:woody spatial regime boundaries by calculating spatial covariance between percent woody plant and grass cover for each raster cell in 1,739-hectare moving window (139 × 139 pixels; Uden et al., 2019). This window size encompasses a broad-scale radius at which grassland birds are known to respond to woody plant encroachment (Cunningham and Johnson, 2006; Thompson et al., 2014; Cunningham and Johnson, 2019; Roberts et al., 2022) while also being small enough to detect variation within the boundaries of the study area (41,170 ha).

Spatial covariance ranges continuously from positive to negative values. Positive values indicate that tree cover and grass cover increase or decrease together across the window; values near zero indicate no spatial relationship between tree and grass cover across the window; and negative values indicate that as tree cover increases across the window, grass cover decreases (or vice versa) (Uden et al., 2019). Thus, strongly negative spatial covariance signifies a spatial regime boundary, where trees and grass are spatially segregated. Near-zero spatial covariance signifies core areas of spatial regimes. To make spatial covariance values comparable across years, we divided the spatial covariance value for each raster cell at each moving window extent by the standard deviation of spatial covariance for each year from 1991 to 2017.

2.4. Hypothesis tests

We tested two hypotheses (H1: spatialtemporal synchrony between grass:woody and bird community boundaries; H2: bird community boundary strength will decline as the number of fires increases) by modeling the response of GAM-predicted wombling R^2 values to spatial covariance and fire history (Fig. 2). To reduce temporal autocorrelation issues, we analyzed a subset of years when bird data was collected. Specifically, we overlayed GAM-predicted wombling R^2 rasters from 1991, 2005, and 2017, spatial covariance rasters from 1991, 2005, and 2017, and fire history rasters with cumulative fire history from 1984 – 1991, 1984 – 2005, and 1984 – 2016. To reduce issues with spatial autocorrelation, we randomly sampled 10% of the pixels within each year's raster. This yielded 15,528 samples (i.e., pixels) total.

With these 15,528 samples, we developed a hierarchical generalized additive model (HGAM) using the "mgcv" package (Wood et al., 2017;

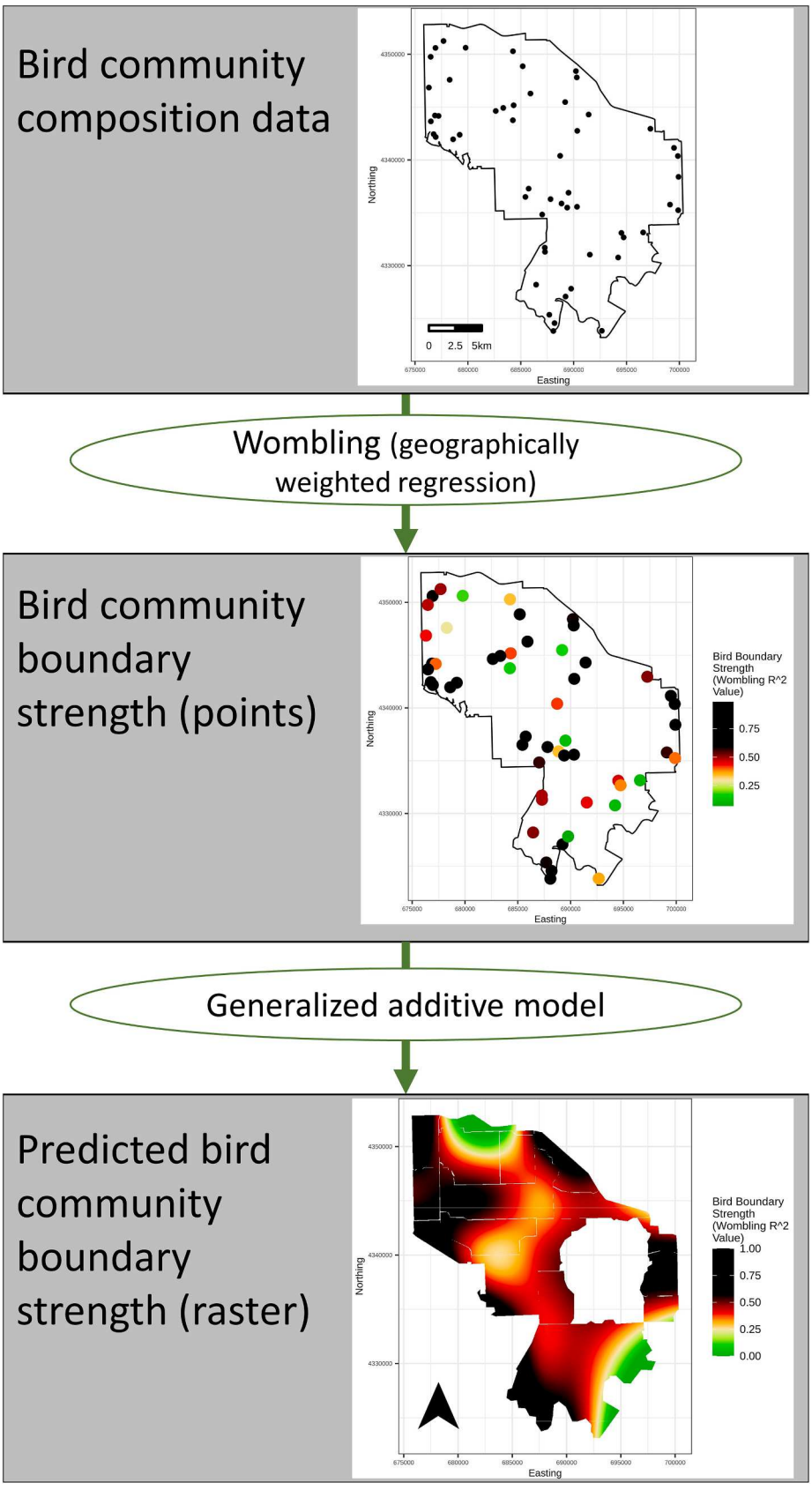

Fig. 1. Visual representation of the workflow for identifying spatial regime boundaries at Fort Riley Army Base, Kansas, USA, using bird community data. Gray rectangles contain description of the data at each stage of the workflow, and green ovals show the calculation or model used to generate the subsequent stage. The first stage is raw bird community composition data collected from field surveys. Then we used wombling (a geographically weighted regression) to calculate bird community boundary strength for each survey location. Finally, we used a generalized additive model to predict bird boundary strength across a continuous raster surface. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

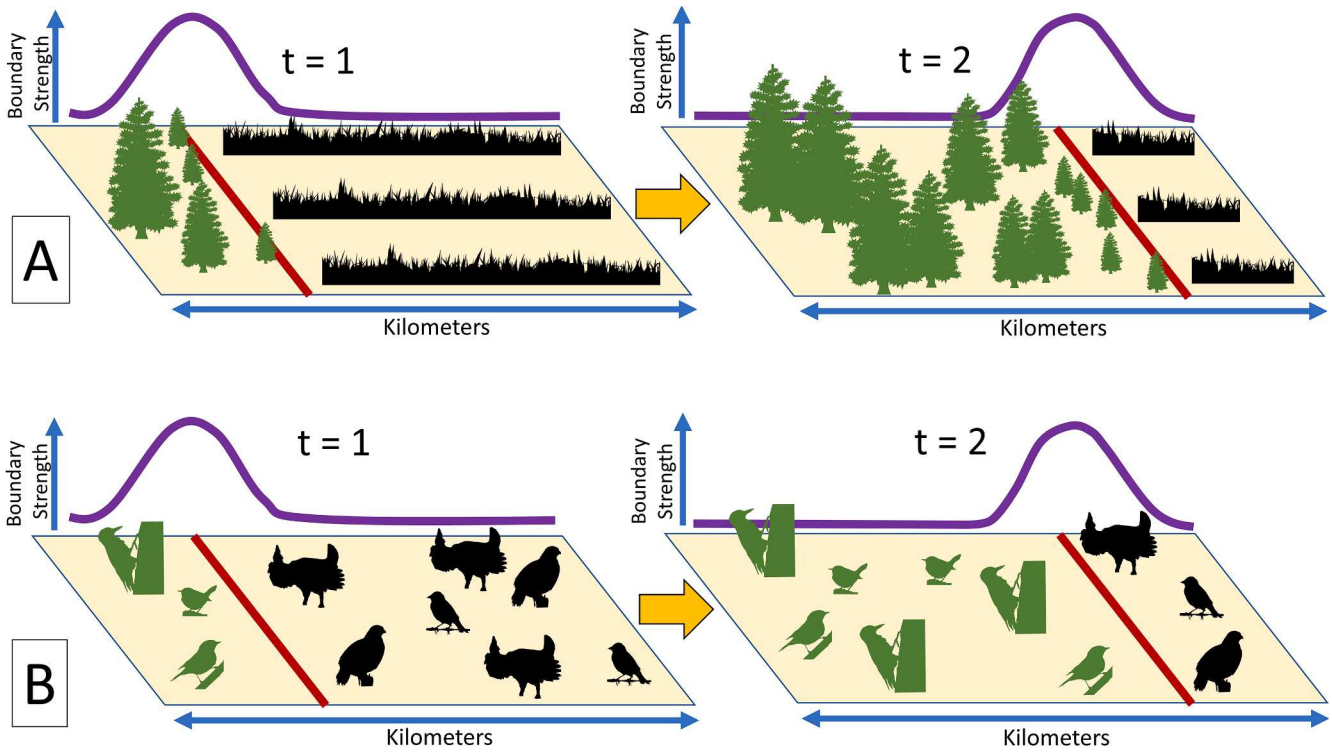

Fig. 2. Conceptual representation of the first hypothesis (H1): spatial regime boundaries identified via independent vegetation and animal datasets will synchronize in space and time. Parallelograms represent a two-dimensional landscape at two time steps (t = 1, t = 2). Green icons represent (A) woodland vegetation regimes and (B) woodland bird community regimes. Black icons represent (A) grassland vegetation regimes and (B) grassland bird community regimes. Purple lines represent the signal strength of statistically identified spatial regime boundaries between woodland and grassland regimes, and red lines indicate where on the landscape these boundaries manifest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Pedersen et al., 2019). In the HGAM, we set GAM-predicted wombling R^2 values as the response variable and used restricted maximum likelihood (Pedersen et al., 2019). We set spatial covariance (H1) and number of fires (H2) as smoothed predictor variables (thin plate splines). We allowed intercepts to vary by year (thin plate spline).

3. Results

3.1. Bird community boundaries

Between 1991 and 2017, surveyors recorded 99 bird species. Calculated wombling R^2 values ranged from 0 to 0.99. The GAM for predicting wombling values onto continuous surfaces explained 38% of deviance (Table S1). Per expectations, GAM-predicted wombling R^2 values revealed two major spatial regimes in the study area: a 'crescent' of grassland regime in the north and central portion of the study area and a forest regime in the southeast of the study area (Fig. 3A). The northernmost portion of the grassland regime remained remarkably stable throughout the study period (Fig. 3A). The western boundary of the central portion of the grassland crescent constricted; but the eastern boundary expanded slightly (Fig. 3A). There is some evidence that the southern portion of the grassland regime also expanded (Fig. 3A).

3.2. Vegetation boundaries

Across the study area and period, scaled spatial covariance values ranged between −2.92 and −0.02 (Fig. 3B). As expected, grass:woody boundary strength was weakest (approximately 0 scaled spatial covariance) in the north, north-central portions of the study area, corresponding with the grassland regime (Fig. 3B). Conversely, grass:woody boundary strength was strongest in the south, corresponding with the forest regime (Fig. 3B). Between 1991 and 2005, the grassland regime contracted considerably, especially at its northwestern and southern boundaries, but between 2005 and 2017, the grassland regime expanded back to a similar extent as in 1991—although it did not reclaim its southern extent.

3.3. Fire history

The cumulative number of fires per pixel ranged from 0 to 9. There were 7 fires between 1984 and 1991, 22 fires from 1984 to 2005, and 66 fires from 1984 to 2016. There were more fires in the north and northeast of the study area, corresponding to the stable grassland regime area in the bird community boundaries and the grass:woody boundaries (Fig. 3C). There were very few fires in the southern portion of the study area, which corresponded with the forest regime and the woody plant encroachment at the southern grassland regime boundaries (Fig. 3C).

3.4. Hypothesis tests

Both of our hypotheses were supported: bird community and vegetation boundaries synchronized in space and time (H1), and grassland bird communities stabilized in space as fire frequency increased (H2). That is, where there were stronger grass:woody vegetation boundaries, there were stronger bird community boundaries, and where there were more fires, there were weaker bird boundaries. The HGAM testing these hypotheses explained 38% of deviance (Table S2). Vegetation boundary strength had a roughly quadratic relationship with bird community boundary strength (effective degrees of freedom, EDF = 8.9; $F = 967$; $P < 0.01$). Starting at very weak grass:woody boundary strength (approximately −0.25 scaled spatial covariance), bird boundary strength rapidly increased and then peaked at relatively weak grass:woody boundary strength (approximately −0.75 scaled spatial covariance; Fig. 4A. After this peak, bird boundary strength declined steadily

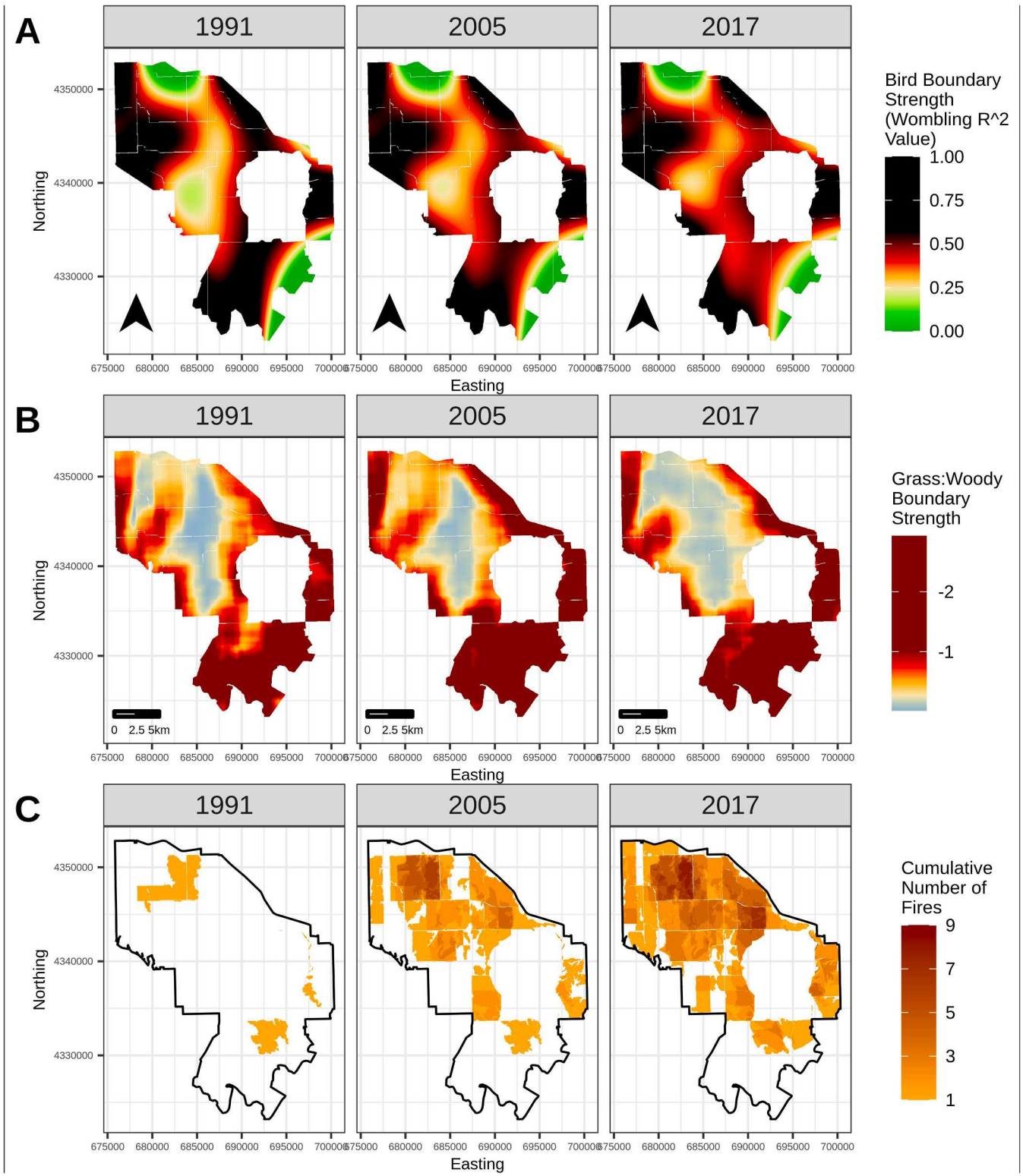

Fig. 3. Tracking spatial regimes within Fort Riley Army Base, Kansas, USA from 1991 – 2017. (A) Bird community boundaries identified via generalized additive model predicted wombling R^2 values. Color shift from green to black (increasing wombling R^2 values) indicates increasing boundary strength. (B) Vegetation (grass: woody) boundaries at a 1,739 ha moving window size. Colors indicate scaled (divided by standard deviation annually) spatial regime boundary strength, with warmer colors (negative spatial covariance values) representing greater boundaries strength and values near 0 representing lack of boundaries. (V) Fire history indicated by the cumulative number of fires that occurred in each pixel between 1984 and 1991, 1984 – 2005, and 1984 – 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

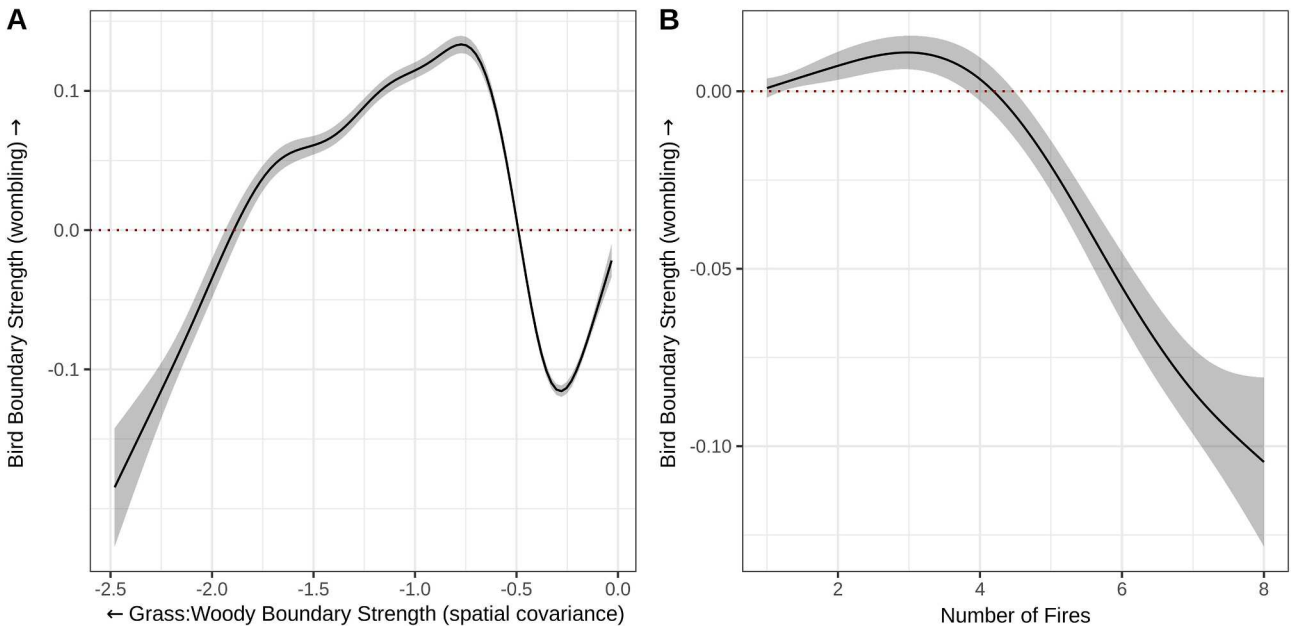

Fig. 4. Hierarchical generalized additive model outputs for two hypothesis tests at Fort Riley Army Base, Kansas, USA from 1991 to 2017. (A) Relationship between bird community boundary strength (wombling R^2 values) and grass:woody spatial regime boundaries (scaled spatial covariance at 1,739 ha moving window size). The grey ribbon indicates 99% confidence limits. Higher R^2 values indicate greater bird community boundary strength, and increasingly negative spatial covariance values indicate increasing grass:woody boundary strength. (B) Relationship between bird community boundary strength and fire history (cumulative number of fires per 30 m^2 pixel). The grey ribbon indicates 99% confidence limits.

and then declined rapidly at the highest grass:woody boundary strengths (Fig. 4A). Fire history had a roughly quadratic relationship with bird community boundary strength (EDF = 3.6; $P < 0.01$; Fig. 4B). Areas with 0 – 3 fires were associated with slightly higher bird boundary strength, but as the number of fires increased from 5 to 8, bird boundary strength decreased (Fig. 4B).

4. Discussion

Both our hypotheses were supported: vegetation and animal community boundaries synchronized in space, and as the number of fires increased, grassland bird communities stabilized in space and time. Boundaries in bird communities clearly manifested when and where they were expected to. For instance, grassland bird community boundaries contracted as expected in response to woody plant encroachment, remained stable in response to negative feedbacks from fire, and expanded where fire treatments killed woody plants and restored grasslands. Conversely, woodland bird community boundaries remained stable in the historically forested portion of the study area and displaced grassland bird regimes where few to no fires occurred and woody vegetation displaced grasses. This indicates our workflow successfully tracked spatial regimes via animal community data and can be incorporated into the 'tracking spatial regimes' approach alongside vegetation data. Our workflow's success is further highlighted by the fact that, despite the noisiness inherent in animal community data and documented idiosyncratic bird species responses to woody plant encroachment and fire (Thompson et al., 2014; Cunningham and Johnson, 2019), spatial boundaries derived from a community of 99 bird species demonstrated clear responses to shifting vegetation and fire history over 26 years.

Tracking spatial regimes with animal community data pixel-by-pixel and year-by-year adds to our ability to quantify a system's ecological resilience by detecting early warnings of eroding resilience. The pursuit of early warnings is central to quantifying resilience (Angeler and Allen, 2016; Eby et al., 2017; Majumder et al., 2019), and Allen et al. (2016) proposed the delineation of spatial regime boundaries as a critical step in advancing resilience quantification. To illustrate—resilience theory predicts that changes in vegetation boundaries may lag behind changes in animal community boundaries (Kent et al., 2013; Allen et al., 2016). This is reflected in our results: grassland bird communities occupied a much narrower spatial extent than the grass:woody boundaries would have suggested: that is, grassland bird communities were (spatially) nested within grass:woody boundaries. Similarly, in areas where greater numbers of fire treatments were applied and grasslands displaced woodlands, grassland bird communities did not expand to the full extent of the new grassland boundaries. This means contracting animal community boundaries (e.g., grassland bird communities being displaced by woodland bird communities) alongside vegetation boundaries may provide an earlier signal of eroding resilience than tracking vegetation boundaries alone (Andersen and Steidl, 2019; Roberts et al., 2022). Also, animal community boundaries may not respond until sufficiently large-scale management occurs (Severson et al., 2017; Olsen et al., 2021). Adding to recent studies showing spatial regimes can be tracked at subcontinental scales (Roberts et al., 2019), we show how tracking spatial regimes via animal community data now allows for resilience quantification at the scale of baseball diamonds (900 m^2 pixels).

Regarding implications relevant to grassland ecosystems, bird community boundaries responded to both woody plant encroachment and fire treatments in expected and interpretable ways. Bird community boundary strength quickly increased and peaked at relatively weak grass:woody boundary strength. This parallels grassland birds' high sensitivity to woody plant encroachment. Many grassland birds will avoid areas with <1% tree cover within a 1,000 m radius (Thompson et al., 2014), some grassland bird species will avoid areas with >2 trees per hectare (Lautenbach et al., 2017), and landscape-scale tree cover far outweighs the importance of microhabitat characteristics for grassland bird nest survival and community composition (Chapman et al., 2004; Fuhlendorf et al., 2017). Likewise, grassland bird community boundaries remained stable where fire occurred every 4–6 years on average (i.e., 5–8 cumulative fires between 1984 and 2016), but they contracted when fire occurred less than every 6 years (0–3 cumulative fires between 1984 and 2016). This echoes decades of research on fire return interval effects on the maintenance of grassland vegetation and bird communities. In tallgrass prairie, fire return intervals of 3 years are the

minimum necessary to maintain grassland regimes in the face of woody plant encroachment (Ratajczak et al., 2016; Fogarty et al., 2021). Increased heterogeneity and removal of trees resultant from fire is known to increase grassland bird diversity and abundance (Fuhlendorf et al., 2006). That bird community boundaries responded in expected and interpretable ways further supports the applicability of the animal community data to the tracking spatial regimes approach and resilience-based management.

4.1. Conclusion

We showcase how tracking spatial regime boundaries with both vegetation and animal community data can inform resilience-based management strategies. Management predominately targets vegetative or abiotic aspects of a system (via fire treatments, brush management, etc.; Scholtz et al., 2021), and even relatively small-scale management can produce short-term desired responses in vegetation regimes. But because animal communities are often sensitive to particular plant compositions and structures (Andersen and Steidl, 2019), management often needs to reach a critical spatial scale or extent to effectively maintain or restore animal components of spatial regimes. By incorporating animal community data into the tracking spatial regimes approach, one can now ask questions such as "what is the minimum grassland size necessary to manifest or maintain a grassland bird regime?" or "what scale of management causes an expansion of desirable animal spatial regimes?". Our approach will be especially useful for motivating spatially-explicit conservation of animal communities that require large-scale, unfragmented landscapes, such as grassland, sagebrush steppe, and savanna (Fuhlendorf et al., 2017; Severson et al., 2017). This a critical need as boundaries between ecoregions and biomes are being redrawn globally (Roberts et al., 2019).

Data availability statement

Vegetation data used in this study are freely available via the Rangeland Analysis Platform (https://rangelands.app/products/#great-plains-data-download), and fire history data is freely available via the Monitoring Trends in Burn Severity dataset (https://www.mtbs.gov/). Raw bird community composition data and bird survey coordinates supporting this research may be requested from the US Department of Defense Fort Riley Army Base, Environmental Division of Public Works. We provide vegetation data, fire data, calculated wombling values, and reproducible code (LivingLandscapes, 2022) on Zenodo at https://doi.org/10.5281/zenodo.5904017.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding for this research was provided by the US Department of Defense Strategic Environmental Research and Development Program (W912HQ-15-C-0018), the University of Nebraska's Institute of Agriculture and Natural Resources, and Arkansas Game and Fish Commission through cooperative agreement 1434-04HQRU1567. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108567.

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