Tracking spatial regimes as an early warning for a species of conservation concern

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Abstract. In this era of global environmental change and rapid regime shifts, managing core areas that species require to survive and persist is a grand challenge for conservation. Wildlife monitoring data are often limited or local in scale. The emerging ability to map and track spatial regimes (i.e., the spatial manifestation of state transitions) using advanced geospatial vegetation data has the potential to provide earlier warnings of habitat loss because many species of conservation concern strongly avoid spatial regime boundaries. Using 23 yr of data for the lek locations of Greater Prairie-Chicken (*Tympanuchus cupido*; GPC) in a remnant grassland ecosystem, we demonstrate how mapping changes in the boundaries between grassland and woodland spatial regimes provide a spatially explicit early warning signal for habitat loss for an iconic and vulnerable grassland-obligate known to be highly sensitive to woody plant encroachment. We tested whether a newly proposed metric for the quantification of spatial regimes captured well-known responses of GPC to woody plant expansion into grasslands. Resource selection functions showed that the grass:woody spatial regime boundary strength explained the probability of 80% of relative lek occurrence, and GPC strongly avoided grass:woody spatial regime boundaries at broad scales. Both findings are consistent with well-known expectations derived from GPC ecology. These results provide strong evidence for vegetation-derived delineations of spatial regimes to serve as generalized signals of early warning for state transitions that have major consequences to biodiversity conservation. Mapping spatial regime boundaries over time provided interpretable early warnings of habitat loss. Woody plant regimes displaced grassland regimes starting from the edges of the study area and constricting inward. Correspondingly, the relative probability of lek occurrence constricted in space. Similarly, the temporal trajectory of spatial regime boundary strength increased over time and moved closer to the observed limit of GPC lek site usage relative to grass:woody boundary strength. These novel spatial metrics allow managers to rapidly screen for early warning signals of spatial regime shifts and adapt management practices to defend and grow habitat cores at broad scales.

Key words: early warning; global environmental change; grassland; Greater Prairie-Chicken; lek; regime shift; screening; spatial regime; state transition; woody plant encroachment.

INTRODUCTION

Regime shifts (i.e., state transitions) are occurring around the world and at the scale of biomes (Roberts et al. 2019). The transitions between alternative states (i.e., regime shifts) are fundamental changes in the

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ecosystem structures and functions that species rely upon to survive and reproduce (Biggs and Carpenter 2009, Allen et al. 2016, Chambers et al. 2017). For example, the sagebrush steppe of North America is undergoing regime shifts from shrublands to conifer woodlands and annual grasslands (Miller et al. 2011, Coates et al. 2016). As their requisite shrubland regime shrinks, sagebrush-obligate species (e.g., Sage-Grouse, *Centrocercus* spp.) show corresponding declines in population and range (Connelly et al. 2004, Knick and

Connelly 2011). Similarly, the Great Plains of North America are undergoing biome-scale regime shifts from grasslands to woodlands (Engle and Coppedge 2008, Garmestani 2020). Over the past 50 yr, grassland-obligate birds have shown the greatest declines in numbers among all guilds in North America (Rosenberg 2019). These examples reflect the scale and scope of contemporary wildlife conservation, and they challenge the conservation community to rapidly mobilize to navigate regime shifts and avoid their consequences to biodiversity and species of conservation concern.

Recent advances in spatial early warning indicators of regime shifts have strong potential to address these conservation issues (Nijp et al. 2019). Early warning indicators provide signals of potentially irreversible change prior to their occurrence to allow managers to avoid regime shifts and "turn back from the brink" (Biggs et al. 2009). Spatial early warning indicators harness the fact that ecological regimes exhibit strong spatial order (Allen et al. 2016, Roberts, 2018a, Uden et al. 2019). This order manifests as "spatial regimes" (Sundstrom et al. 2017). Spatial regimes are defined as spatial extents with relative homogeneity in structure and composition that have identifiable boundaries at a given scale (Uden et al. 2019). The boundaries of spatial regimes can predictably move or expand at the expense of a neighboring spatial regime (e.g., displacement of a woodland regime with a grassland regime) or contract and disappear (e.g., a sagebrush steppe regime is being invaded by an annual grass-dominated regime; Uden et al. 2019). That is, movements of spatial regime boundaries are the spatially explicit manifestation of regime shifts (Roberts et al. 2019). This improves upon other spatial early warning indicators that did not provide spatial context (i.e., detection of regime boundary or tracking), used univariate indicators that produce spurious signals (Burthe 2016), and required a sufficient proportion of a landscape to experience a regime shift before providing a signal (van de Leemput and van Nes 2015). When spatial regimes move, expand, or contract, resilience theory predicts that species reliant on a specific regime will respond by relocating or becoming locally extirpated where the required regime was displaced (Allen et al. 2016, Roberts et al. 2019). A class of new spatial early warning indicators moves from "diagnosing" regime shifts to "screening" for regime shifts and enables mapping and tracking changes in boundaries between spatial regimes (e.g., grasslands, woodlands, and shrublands) at scales ranging from local sites to biomes (Uden et al. 2019). Managers could potentially use the screening workflow to map spatial variations in vegetation regimes associated with life-history requirements of species and identify habitat "cores" in which to prioritize management (Uden et al. 2019). Then, managers could monitor changes in spatial regime boundaries to provide early warning signals of habitat loss (Roberts et al. 2018a).

For spatial early warnings of regime shifts to be useful for identifying changes in available habitat for species, species must respond (proactively, in tandem, or reactively) to spatial regimes, particularly their boundaries, at identifiable scales (Allen et al. 2016). Species with strong state affinities should strongly avoid boundaries between spatial regimes, possibly to the point of failing to occur at or near boundaries. For example, Prairie-Chickens (*Tympanuchus* spp.), an iconic grassland-obligate species of the Great Plains of North America, are experiencing range-wide population declines because of habitat loss due in large part to woody plant encroachment into grasslands (Fuhlendorf et al. 2002, Miller et al. 2017). Decades of studies show that Prairie-Chickens require grasslands and avoid even minimal tree cover at broad scales (Merrill et al. 1999, Niemuth 2000, McNew and Prebyl 2012, Hovick et al. 2015, Lautenbach et al. 2017). Range-wide population declines are also linked to tree invasion of grasslands (Engle et al. 2008, Fuhlendorf et al. 2017). Given the evidence for Prairie-Chickens' avoidance of trees at broad scales and requirement of large-scale grasslands, tracking spatial boundaries between grass-dominated and woody plant-dominated regimes should provide spatial early warning signals of habitat loss for Prairie-Chickens (Falkowski et al. 2017).

Here, we used a long-term dataset to track changes in spatial boundaries separating grass:woody regimes over time, and then test, for the first time, whether these boundaries serve as an early warning signal for habitat loss. We used 23 yr of Greater Prairie-Chickens' (*Tympanuchus cupido*; GPC) lek location data at Fort Riley Army Base, Kansas, USA. Given the breadth of knowledge on GPC ecology, we expect GPC lek site usage to (1) respond to spatial boundaries between grass:woody regimes at broad scales rather than fine scales, and (2) exhibit high sensitivity and avoidance of the spatial boundaries where grassland-dominated regimes end and the woody plant-dominated regimes begin. We define "usage" as probability of lek occurrence at a location while acknowledging that male GPC lek site usage is a direct and often lagged response to female GPC nest-site selection (Fuhlendorf et al. 2002, Gehrt and Sullins 2020). Given the scale, sensitivity, and directionality of GPC lek site usage relative to grass:woody spatial regime boundaries, we demonstrate opportunities for new spatial metrics to serve as generalized early warnings of state transitions (i.e., regime shifts) and their implications for conservation.

METHODS

Study site

We conducted this study at Fort Riley Army Base, Kansas, USA, which is a military reservation of approximately 41,170 ha in size. Fort Riley lies in the Flint Hills ecoregion of the North American Great Plains. The Flint Hills can support two major alternative vegetation regimes: grass-dominated regime and woody

plant-dominated regime (Engle et al. 2008). Historically, these two vegetation regimes were restricted to areas that could escape fire (e.g., ravines, rocky outcroppings). Due to fire suppression and tree plantation by European colonizers, woody plant-dominated regimes are displacing grass-dominated regimes across the Great Plains and within Fort Riley (Garmestani et al. 2020). However, at Fort Riley, random fire ignitions from military training, wildfire, prescribed fires, haying, and mechanical tree removal also act to maintain grass-dominated regimes in certain areas across the base. Fort Riley itself is dominated by a never-ploughed tallgrass prairie. But it is surrounded by urban and forested riparian areas to the south and east, a large reservoir to the west, and a mix of crop and rangelands to the north. These barriers effectively isolate the population of GPC at Fort Riley. Overall, Fort Riley is an isolated and relatively contiguous grassland-dominated regime.

Data collection

Spatial early warnings of grass:woody transitions.—We used the approach suggested by Uden et al. (2019) to map and track spatial boundaries between grassland- and woodland-dominated regimes. This approach utilizes spatial covariance between the proportional cover of pairs of major plant functional groups (e.g., tree vs. grass cover) as a screening metric (Wagner 2003). Spatial covariance applies a core principle of resilience theory: alternative vegetation states can coexist at certain scales (e.g., landscapes), but they cannot coexist at others (e.g., a grassy state cannot exist within a patch of close-canopied forest; Allen et al. 2016). Spatial covariance measures the degree of coexistence between two plant functional groups at a given scale (i.e., moving window kernel size), thereby acting as an edge-detection technique for spatial regimes and an early warning signal of regime shifts (Roberts et al. 2018a, Uden et al. 2019). The more the two functional groups are negatively associated with one another in space (i.e., one increases while the other decreases), the more negative their spatial covariance, whereas the more the two functional groups are positively associated with one another in space (i.e., they increase or decrease together), the more positive their spatial covariance. The value of spatial covariance is 0 means that no spatial relationship exists between two functional groups. As spatial covariance is a continuous metric, hereafter, we refer to spatial covariance as "spatial regime boundary strength," with more negative values being "strong" and values close to zero (e.g., >−1) being "weak" boundaries. Used over time, spatial covariance tracks where one regime is advancing, in geographic space, at the expense of the other (Uden et al. 2019).

For spatial covariance data inputs, we obtained percent perennial forb and grass (hereafter, perennial) cover and percent tree cover data for the area in and around Fort Riley from 1994 to 2017 at approximately 30-m resolution (0.09 ha) from the Rangeland Analysis Platform (version 1; Jones et al. 2018). Prior to analysis, we masked all pixels (Jones et al. 2018) classified as cropland, developed, or watered as mentioned in the 2011 National Land Cover Database (Homer et al. 2015). We computed spatial covariance between percent perennial and percent tree cover within moving windows of nine sizes (i.e., scales) in Google Earth Engine (Gorelick et al. 2017) by using the covariance reducer function (Pebay 2008). We chose window sizes of 0.81, 15, 98, 182, 292, 620, 1,030, 1,274, and 1,592 ha, which range from the finest scale at which spatial covariance can be calculated when the given resolution is 30-m pixel (3×3 pixels = 0.81 ha) up to the broader scales identified as important in GPC lekking and habitat ecology (Fuhlendorf et al. 2002, McNew et al. 2012, Hovick et al. 2015). We rescaled spatial covariance values (by dividing values by their standard deviation, but did not center on zero) by scale and year to ensure comparability across scales.

GPC lek surveys.—Personnel from the Fort Riley Army Base Conservation Office conducted GPC lek surveys between 1 March to 15 April annually from 1994 to 2017. Surveys began 30 min before sunrise and terminated 90 min after sunrise. Surveyors collected data only when wind velocities were <19 kph and precipitation was not falling. Surveyors drove established survey routes two to three times every year (Appendix S1: Fig. S1). Route revisits varied due to logistical constraints imposed by the military training and differences in annual budgets. At approximately 1.6 km intervals, surveyors stopped and listened or visually searched for active leks within 1 km of survey routes. In all, surveys covered approximately 33,058 ha. Surveyors flushed all observed leks to determine the approximate spatial center of the lek and recorded spatial coordinates. We removed satellite leks (i.e., leks where surveyors recorded <3 males) from our analyses.

Analysis

Scale(s) of GPC lek site usage response to grass:woody spatial regime boundaries.—We used model selection to identify the scale(s) at which GPC lek site usage responded to spatial early warnings of grass:woody transitions. We used binomial generalized mixed models via the "glmer" function in R package "lme4" (Bates et al. 2007) to estimate resource selection functions (RSFs; Manly et al. 2002). Model response variables were observed leks (present = 1) and 10 randomly selected locations within 1 km of survey routes (present = 0; Appendix S1: Fig. S1) to represent available resources (habitat). We randomly selected 10 locations for every observed lek to ensure model convergence (Monteith et al. 2018).

We developed RSF models with 10 candidates. Nine models consisted of grass:woody spatial covariance at single scale and a random effect in which we allowed the intercept to vary by year. The final model was a null that contained only the random effect. We assumed that the observed leks were spatially independent because (1) male GPC choose lek sites based on dynamic disturbance processes and habitat selection of female GPC and are therefore non-stationary in space and time and (2) we detected no spatial autocorrelation in our models (Appendix S1: Fig. S1; Hovick et al. 2015). We used Akaike's Information Criterion for small sample sizes (AICc) to rank models. We considered top-ranked model(s) (i.e., models with <2 ΔAICc) as the scale(s) at which GPC lek site usage responded to spatial regime boundaries.

Sensitivity and directionality of GPC lek site usage to grass:woody spatial regime boundaries.—We quantified GPC lek site usage response to grass:woody spatial regime boundary strength by estimating probabilities of lek occurrence in response to grass:woody spatial covariance at identified scales. We estimated both the marginal (fixed effects only) and conditional (fixed and random effects) relative probabilities of lek occurrence. We estimated 95% confidence limits for both marginal and conditional probabilities via 10,000 bootstrap simulations by using the "bootMer" function in "lme4." We assessed top-model fit by estimating pseudo-R^2 values using the "r.squaredGLMM" function in R package "MuMIn" (Nakagawa and Johnson 2017, Barton and Barton 2019).

Grass:woody spatial regime boundaries as spatial early warnings for declining probability of GPC lek occurrence.—We demonstrated how grass:woody spatial regime boundaries can serve as spatial early warnings of declining probability of GPC lek occurrence via two methods: (1) map and track changes in grass:woody boundaries over time, and (2) assess the trajectory of grass:woody boundary strength over time. In the first method, non-stationarity in grass:woody boundaries, especially when boundaries move in a persistent direction, is the early warning signal of a regime shift and declining probability of GPC lek occurrence (Roberts et al. 2019, Uden et al. 2019). In the second method, increasing grass:woody boundary strength (i.e., decreasing spatial covariance) over time that approaches the limit of observed GPC lek site usage relative to grass:woody boundary strength is the early warning signal.

To map and track changes in grass:woody boundaries over time, we visually compared changes in mapped spatial covariance over multiple years. We specifically searched for boundary constriction around and fragmentation of formerly intact grassland areas. We also mapped relative probabilities of lek occurrence using the top-ranked model of GPC lek occurrence response (i.e.,

identified scale[s]) to spatial covariance to compare changing grass:woody boundaries with predicted changes in probability of GPC lek occurrence.

To assess the trajectory of grass:woody boundary strength over time, we calculated the median and the 25th and 75th quantiles of spatial covariance at identified scale(s). Then, we determined if grass:woody boundary strength was increasing, decreasing, or remaining stable using a generalized least squares regression. We set median spatial covariance at identified scale(s) as the response variable and time (year) as the predictor variable. We used the median instead of the mean because of the skewed distribution of spatial covariance. We set the observed limit of GPC lek site usage relative to grass:woody boundary strength as the lowest observed value of spatial covariance at which GPC leks occurred at any time during the study.

Results

Scale(s) of GPC lek site usage response to grass:woody spatial regime boundaries

The range of the number of leks recorded annually ranged from 3 to 23, with an average of approximately 16 leks. Model selection showed that GPC responded to grass:woody spatial regime boundaries most clearly at the 182 ha scale (95% AICc weight; Table 1). However, there was also support for the 292 ha scale (5% AICc weight; Table 1). The third- and fourth-ranked models were 620 ha and 98 ha, respectively—the scales directly above and below the top-ranked and second-ranked scales (Table 1). The broadest scales were next in support, and the finest scales were ranked last (Table 1). This suggests that our model set encompassed a sufficient range of scales. For simplicity's sake, we only consider the top-ranked (182 ha scale) model for the remainder of this research paper. We detected no spatial autocorrelation in the top-ranked model (Appendix S1: Fig. S2).

Sensitivity and directionality of GPC lek site usage to grass:woody spatial regime boundaries

At the 182 ha scale, the greatest relative probability of GPC lek occurrence (>40% relative probability) was near to 0 spatial covariance, where no grass:woody spatial regime boundaries occurred (Fig. 1, Appendix S1: Fig. S3). Relative probability of GPC lek occurrence strongly decreased with increasing grass:woody boundary strength (i.e., negative spatial covariance; Fig. 1). This relationship was similar and significant for all models (scales; window sizes), although to different degrees (Appendix S1: Table S1). We did not find any leks below −0.87 spatial covariance or above 0.1 spatial covariance (Fig. 1). Marginal and conditional pseudo-R^2 values for the top model were 0.807 and 0.810, respectively.

TABLE 1.   Model selection results for identifying functional scales of Greater Prairie-Chicken lek response to grass:woody spatial transitions at Fort Riley Army Base, Kansas, USA, for the period 1994–2017.

Model	AICc	ΔAICc	AICc Weight
lek presence ~ SpCov 182 ha + (1|Year)	2,047.17	0.00	0.95
lek presence ~ SpCov 292 ha + (1|Year)	2,052.99	5.83	0.05
lek presence ~ SpCov 620 ha + (1|Year)	2,064.97	17.80	0.00
lek presence ~ SpCov 98 ha + (1|Year)	2,090.52	43.35	0.00
lek presence ~ SpCov 1,030 ha + (1|Year)	2,103.99	56.82	0.00
lek presence ~ SpCov 1,274 ha + (1|Year)	2,136.15	88.99	0.00
lek presence ~ SpCov 1,592 ha + (1|Year)	2,156.63	109.46	0.00
lek presence ~ SpCov 15 ha + (1|Year)	2,214.90	167.73	0.00
lek presence ~ SpCov 0.81 ha + (1|Year)	2,389.72	342.55	0.00
lek presence ~ (1|Year)	2,502.84	455.67	0.00

Notes: "SpCov" indicates "spatial covariance," hectares (ha) indicate scale (window size) at which grass:woody spatial transitions were calculated, and "(1|Year)" indicates a random intercept for time (year).
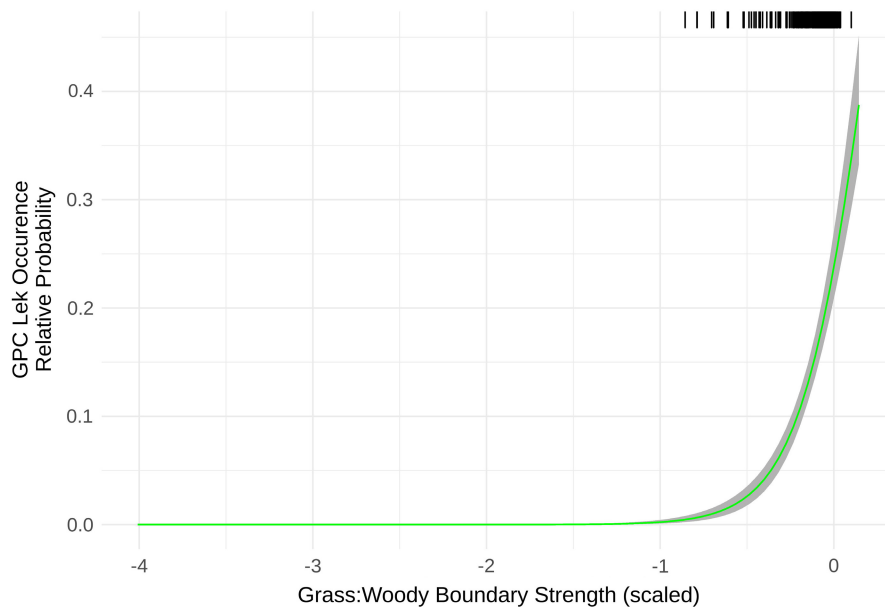

FIG. 1.   Predicted relative probability of Greater Prairie-Chicken lek occurrence based on grass:woody spatial regime boundary strength at the 182 ha scale at Fort Riley Army Base, Kansas, USA, from 1994 to 2017. Grass:woody boundary strength (spatial covariance) values were scaled by dividing them by their standard deviation annually. The green line indicates predicted relative probability from fixed effects, and the gray ribbon indicates 95% confidence limits from 10,000 bootstrap simulations. Black ticks above the graph indicate all spatial covariance values at which leks were observed.

Grass:woody spatial regime boundaries as spatial early warnings for declining probability of GPC lek occurrence

Both methods of using spatial early warning signals of grass:woody boundaries provided early warning signal of declining probability of GPC lek occurrence. Mapped spatial covariance for the period from 1994 to 2017 showed increasing spread and strength of grass:woody spatial regime boundaries (decreasing spatial covariance values) across the study area (Fig. 2, Appendix S1: Figs. S4, S5). Per visual inspection, boundary constriction originated from the edges of the study area and moved toward the center (Fig. 2, Appendix S1: Figs. S4,

S5). This means that the probability of GPC lek occurrence will rapidly decline at the edges of the study area, and it provides an early warning signal of GPC habitat loss in the center of the study area (Fig. 2, Appendix S1: Figs. S4, S5). Correspondingly, model predictions show rapid declines in relative probabilities of lek occurrence at the edges of the study area from 1994 to 2006 (Fig. 2, Appendix S1: Figs. S4, S5). The probability of lek occurrence then constricted and eroded toward the center of the study area (Fig. 2, Appendix S1: Figs. S4, S5).

Temporally, grass:woody boundary strength increased over time and approached the limit of observed GPC lek site usage relative to grass:woody boundary strength
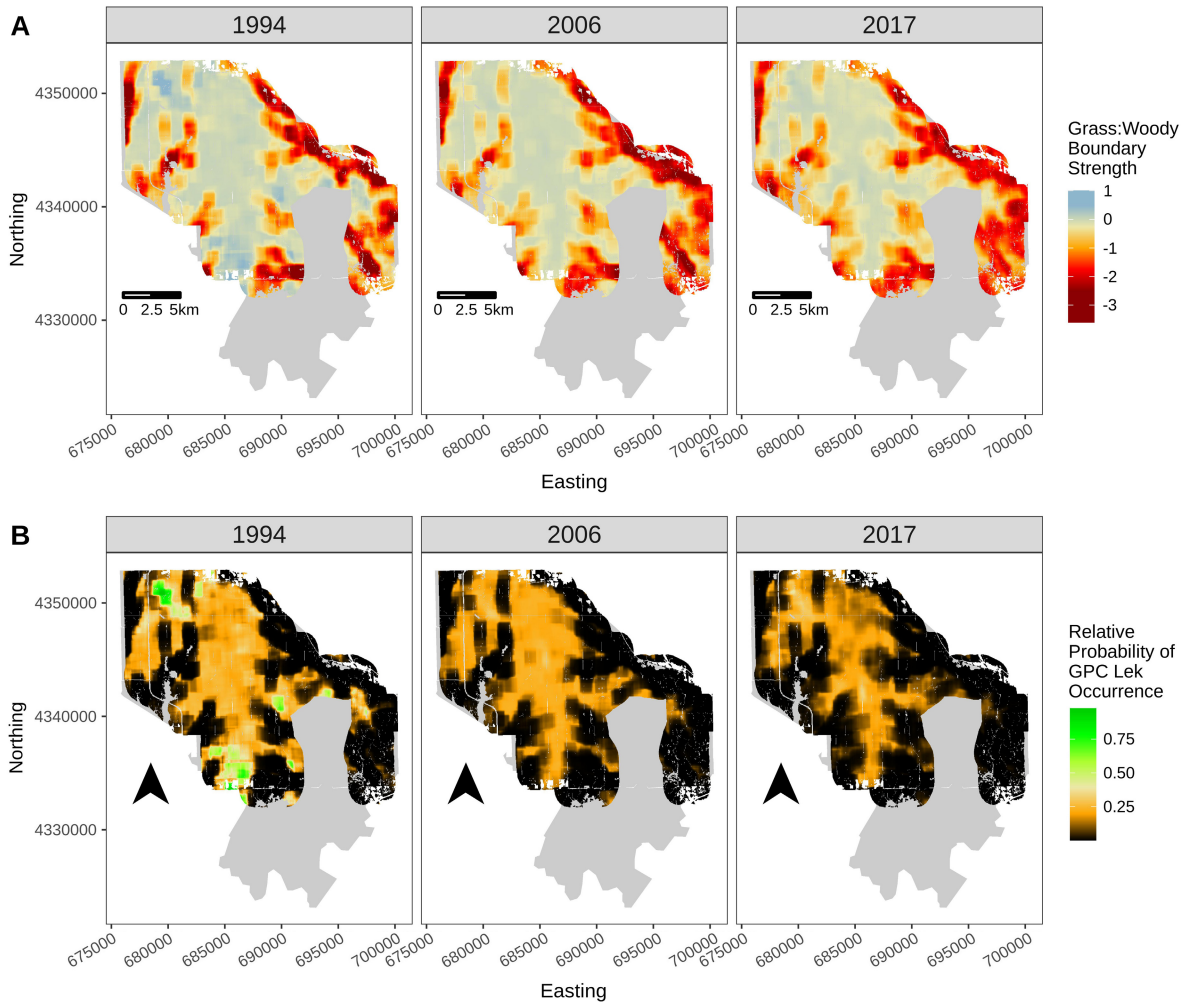
Fig. 2. Mapping and tracking grassland-dominated and woody plant-dominated spatial regime boundaries as a spatial early warning for declining probability of Greater Prairie-Chicken lek location occurrence within Fort Riley Army Base, Kansas, USA, from 1994 to 2017. (Panel A) Movement of grass:woody spatial regime boundaries at a 182 ha scale (moving window size) during selected years of the study. 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. (Panel B) Spatial changes in predicted Greater Prairie-Chicken lek occurrence is based on grass:woody transition strength (see top panel). Colors indicate relative probability of lek occurrence. Gray areas indicate areas within Fort Riley that were not surveyed due to military trainings and urban development.

(Fig. 3). Median spatial covariance decreased by -0.009 per year ($P = 0.063$; $t = -1.958$; df $= 24$; Fig. 3). This means tree regimes increased in geographic extent across the study area, and grass:woody boundaries strengthened as tree density increased (Figs. 2, 3, Appendix S1: Figs. S4, S5). In 1994, 29% of the study area was outside the observed limit of GPC lek site usage. In 2017, 36% of the study area was outside this limit (Fig. 3).

DISCUSSION

Tracking spatial boundaries between alternative grassland-dominated and woody plant-dominated regimes provided spatially explicit early warning signals for habitat loss for Greater Prairie-Chickens. Spatial boundaries between alternative states (i.e., spatial regimes) move, expand, and contract with strong spatial order (Allen et al. 2016, Sundstrom et al. 2017, Roberts et al. 2019, Uden et al. 2019). Greater Prairie-Chickens clearly avoided moving spatial boundaries separating grass-dominated and woody plant-dominated regimes at broad scales. Grass:woody boundary strength explained 80% of variation in the relative probability of lek occurrence. We observed no GPC leks near strong grass:-woody spatial regime boundaries. It is important to note that many drivers, besides woody plant encroachment, influence GPC habitat usage. Examples of these drivers are human disturbance (e.g., military training, haying,
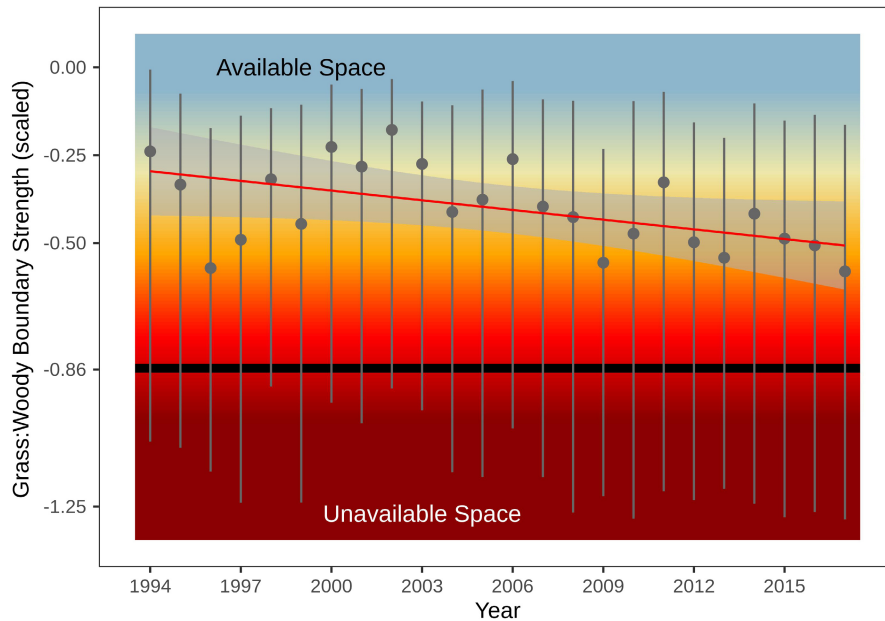
FIG. 3. Temporal trajectory of spatial early warnings of grass:woody regime shifts as an early warning of Greater Prairie-Chicken habitat loss relative to observed limits of Greater Prairie-Chicken lek site usage at Fort Riley Army Base, Kansas, USA, from 1994 to 2017. Black dots are annual medians, and whiskers are the 25th and 75th quantiles of grass:woody spatial regime boundary strength across the study area. The red line and gray ribbon are generalized least squares regression predictions of median and 95% confidence limits of the trajectory of median grass:woody spatial regime boundary strength across the whole study area. Boundary strength values above the black horizontal line (the strongest grass:woody boundary strength at which we observed Greater Prairie-Chicken leks) are "safe operating space" for Greater Prairie-Chicken leks, and strengths below the black line are outside of observed lek site usage relative to grass:woody boundary strength.

tree removal), fires (prescribed fires and not), and intensive drought (e.g., droughts in 2012 and 2013 during our study period). However, our results indicate that nonstationary spatial regime boundaries can serve as clear and broad-scale spatial early warning signal of habitat loss for obligate species of grassland regimes. These findings represent a major advancement beyond simply further understanding of habitat requirements of a species. Spatial early warnings of vegetation regime shifts can be mapped and visually inspected over time via a "screening" workflow (Uden et al. 2019). By using these maps, managers can identify and proactively conserve remaining habitats for vulnerable species and then implement strategic restoration to defend those spaces (Falkowski et al. 2017, Miller et al. 2017, Uden et al. 2019).

For species whose life-history requirements are completely encompassed within a particular regime (e.g., grasslands for Prairie-Chickens, sagebrush for Sage-Grouse, etc.), screening for spatial regime boundaries can provide a quick, broad-scale habitat assessment relative to persistent ecosystem threats (e.g., woodland or annual grass invasion, infilling of trees in savannas; Chambers et al. 2017, Fuhlendorf et al. 2017). Using recent advances in remote sensing, cloud computing, and spatial early warning metrics, Uden et al. (2019) developed a workflow for "screening" for spatial regime boundaries. This workflow is analogous to medical screening for diseases, prior to diagnosis and the onset of signs and symptoms. It also follows the increasingly spatial pursuit of detecting early warning signals of regime shifts in ecosystems (Nijp et al. 2019, Roberts et al. 2019). In the screening workflow, spatial boundaries between alternative states are identified and tracked over time (e.g., via spatial covariance of vegetation functional group pairs, as in this research paper), and the pattern and/or spatial regime boundaries over time are combined with other sources of information to help determine where and when management should be prioritized (Uden et al. 2019). We also show screening and spatial covariance tracks where boundaries are strengthening; for instance, spatial covariance showed where tree density increased at the expense of grass cover at the outermost edges of our study area.

Our results also link the concept of spatial regimes and resilience theory to our understanding of habitat selection. At broad scales, GPC leks simply do not occur where grass:woody spatial regime boundaries occur (Merrill et al. 1999, Niemuth 2000, McNew et al. 2012, Fuhlendorf et al. 2017). As woody plant-dominated regimes moved inward from the edges of our study area, they displaced grassland-dominated regimes in the core of the study area. Correspondingly, GPC usage shrank. The concept of spatial regimes (and resilience theory) encapsulates these phenomena in three predictions: ecological regimes have spatial context, state transitions have strong spatial order, and spatial regimes can move,

expand, and contract in predictable patterns (Allen et al. 2016, Sundstrom et al. 2017, Roberts et al. 2019). Investigations of habitat selection can harness the predictable non-stationarity of spatial regimes to identify boundaries of available habitat near the edges of spatial regimes, track regime or movement of boundary of habitat over time, and identify habitat "cores" near the centers of spatial regimes. Spatial regimes may provide a more objective and biologically relevant method for defining what is "available" vs. "unavailable" to species—especially species that cleave to a specific regime (e.g., GPC to grasslands)—than traditional methods (e.g., minimum convex polygons, kernel density estimates), which rely on where focal species occur rather than their ecological limits (White and Garrott 2012). Spatial regimes also acknowledge that ecosystems are dynamic in space and time, and habitats move, shrink, and expand with spatial regimes (Hovick et al. 2015, Holbrook et al. 2019).

The concept of spatial regime also adds a hierarchical level to the traditional habitat selection concept (Allen and Starr 2017). For example, the four orders of habitat selection processes proposed by Johnson (1980) could be considered nested within a spatial regime. To illustrate, Lautenbach et al. (2017) found a threshold of tree cover above which Lesser Prairie-Chickens' (*Tympanuchus pallidicinctus*) nests did not occur. These areas were simply not usable by Lesser Prairie-Chickens. Likewise, in our study, GPC leks did not occur past a certain level of grass:woody transition strength, which explained the probability of 80% of relative lek occurrence. Greater Prairie-Chickens can only survive and persist within grassland spatial regimes meaning, the current spatial regime and regime boundaries supersede all other habitat attributes (Allen and Starr 2017, Falkowski et al. 2017, Miller et al. 2017). A meta-analysis of habitat selection studies for Sage-Grouse, which belongs to another grouse genus, echoes that Sage-Grouse are habitat generalists within the sagebrush ecosystem. But at the same time, these birds are sagebrush obligates and cannot persist outside shrubland regimes (Smith et al. 2020). It follows that even first-order selection (the geographic range of a species; Johnson 1980) would be dictated by the identity of spatial regime and boundaries (Allen and Starr 2017, Fuhlendorf et al. 2017). But, as spatial regimes manifest at discontinuous scales (i.e., they are scale-dependent phenomena; Allen et al. 2016), future research should investigate how they can be utilized across the scales of habitat selection.

Conclusions

Advances in spatial early warning signal methods allow tracking spatial boundaries between alternative states at local scales to biome scales (Jones et al. 2018, Uden et al. 2019), and advances in technologies provide rapid calculation and public availability of these metrics

(e.g., spatial covariance; see https://rangelands.app/products/data-download and https://rangelands.app/products/#woody-transitions). As regime identity (e.g., grassland, woodland, shrubland) supersedes fine-scale habitat attributes in terms of life-history requirements of species (Chambers et al. 2017, Fuhlendorf et al. 2017, Smith et al. 2020), tracking spatial regimes provides a rapid method for mapping potential habitat that can inform strategic habitat conservation to address undesired regime shifts. Maps of spatial boundaries between alternative states can be used to first identify and "defend the cores" of habitats (i.e., large areas without spatial regime boundaries) of species. Then, management can work to "grow the cores" through targeted restoration of transitioning zones at spatial regime boundaries. The important phases of a potential management workflow would be (1) screen for spatial regime boundaries, (2) identify spatial habitat cores and prioritize maintaining negative feedbacks in cores, (3) restore transition zones surrounding the core in order to grow the core, and (4) continue to track spatial regime boundaries and adapt accordingly. Considering our study area as an example, the center of the study area could serve as a grassland core to prioritize and protect through frequent prescribed fires and local eradication of invasive woody species (Roberts et al. 2018b). In the next step, strategic restoration along the boundaries could grow cores by eliminating grass:woody transition zones to connect with another transition-free area. This workflow offers a strategic assessment and predictive management tool for managing vulnerable species (e.g., GPC) at broad scales in this era of global change and increasing state transitions (Falkowski et al. 2017, Miller et al. 2017). Future work should investigate applications at the scale of biomes and geographic ranges of species.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2480/full

OPEN RESEARCH

Vegetation data used in this study are freely available in the Rangeland Analysis Platform via the process described in the *Methods: Data Collection, Spatial early warnings of grass:woody transitions* subsection. Greater Prairie-Chicken lek location related data supporting this research are available with restrictions and are not accessible to the public or research community. Researchers may contact the US Department of Defense Fort Riley Army Base Environmental Division of Public Works to request data access. We provide vegetation data extracted to present (observed) and absent (randomized locations) lek locations and reproducible code (LivingLandscapes 2021) on Zenodo at https://doi.org/10.5281/zenodo.4774056