

FINAL REPORT

Global Change, Vulnerability and Resilience: Management Options for an Uncertain Future

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KEYWORDS

Ecological resilience, complex systems, vulnerability, Fisher Information, ecological monitoring, spatiotemporal regime shifts, discontinuity analysis

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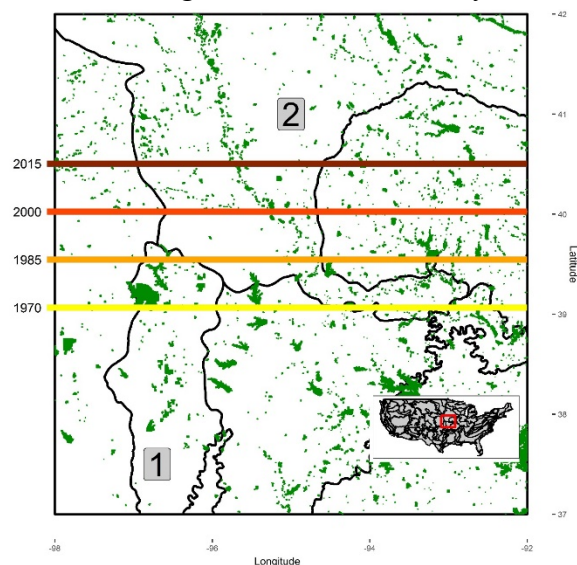
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ABSTRACT

Introduction and Objectives: The Earth has entered a new epoch, the Anthropocene, wherein the footprints of human activity (e.g., eutrophication, acidification, climate change) may manifest in erosion of ecological resilience and consequential losses of ecosystem services. Ecological resilience is the ability of an ecological system to absorb disturbance without experiencing a catastrophic shift into an alternative regime. To allow the Department of Defense (DoD) to predict and adapt to ecological changes that may result in regime shifts and effect individual bases' and the DoD as a whole's ability to carry out their missions, our objectives in this research were to develop models to detect ecological regime shifts in space and time and to develop metrics to quantify ecological resilience and adaptive capacity.

Technical Approach: We used a mixture of sub-continental data (e.g., the North American Breeding Bird Survey) and local datasets (e.g., ecological monitoring data from Eglin Air Force Base and Fort Riley Army Base). We then developed novel statistical tools (e.g., Fisher Information, discontinuity analysis, spatial regimes tracking) and tested existing tools to assess long-term trends in resilience of landscapes, detect and predict ecological regime shifts in both space and time, and identify species vulnerable to decline and extinction, with a focus on the management of DoD properties.

Results: We successfully created methods to detect regime shifts in space and time. Spatial regimes tracked regime shifts that occurred between 1970 – 2015 and across > 500km in central USA. We show tracking spatial regime boundaries can provide decades of early warning of regime shifts. We also generated new methods based on Fisher Information to detect and predict early warnings of regime shifts over time. Finally, we show that rare species contribute to adaptive capacity, and we demonstrate successful usage of resilience metrics to compare and estimate ecological resilience of ecosystems over time and space.



Benefits: Using our methods, the DoD can create resilience-based management frameworks that allows managers to target, and eventually reduce, the uncertainties resulting from global changes. For instance, by tracking spatial regime boundaries across a network of military installations (Figure 1), the DoD could provide early warnings of regime shifts to bases in the path of the changing spatial regimes. This would provide bases decades to adapt to the changes or work to halt the regime shifts.

Figure: Spatial regime boundary movement between 37 – 42 degrees latitude across a network of protected areas covering in central North America. Black lines indicate level III US Environmental Protection Agency ecoregion boundaries, and green polygons indicate protected areas. The ecoregion labeled No. 1 is the Flint Hills ecoregion, and the ecoregion labeled No. 2 is the Western Corn Belt Plains ecoregion. Predicted spatial regime boundaries (colored horizontal lines) correspond with linear prediction for the years 1970, 1985, 2000, and 2015 ($\beta = 0.032 \pm 0.026$ degrees latitude per year; 90% confidence; $F = 4.093$; $P = 0.052$).

EXECUTIVE SUMMARY

Introduction

The Earth has entered a new epoch, the Anthropocene, wherein the footprints of human activity (e.g., overfishing, eutrophication, acidification, climate change) may manifest in erosion of ecological resilience. Ecological resilience is defined as the ability of an ecological system to absorb disturbance without experiencing a catastrophic shift into an alternative regime (Figure 1). Examples of alternate regimes include: a flatland woods existing in a pine savanna or oak-dominated forest, a shallow lake that may exist in a clear, low nutrient, low algae, oxygen-rich state (oligotrophic) versus a turbid, high nutrient, high algae, oxygen-poor state (eutrophic); or a semi-arid terrestrial ecosystem existing in a grassland versus a woody-plant dominated state. Increasing pressures from growing human populations will likely continue to push ecosystems beyond their capacity to cope with stress. Consequently, increasing incidences and magnitudes of regime shifts will likely characterize the Anthropocene and trigger complex social-ecological responses that can transcend scales from local to regional to global. There is also concern that regime shifts will ultimately result in the loss of some of the crucial ecosystem goods and services upon

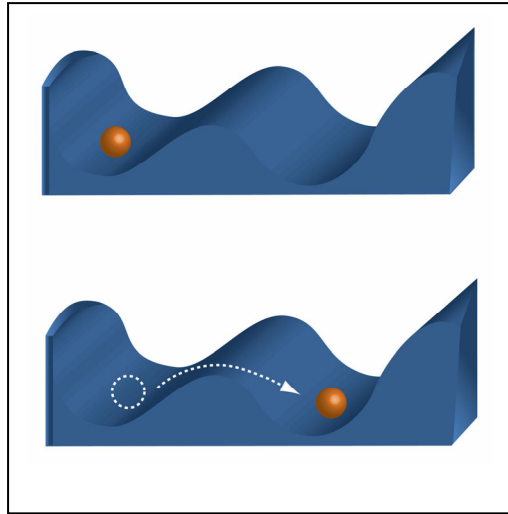


Figure 1. A conceptual diagram of the basins of attraction for two possible ecosystem states, characterized by two different regimes. The position of the ball in the left basin of the upper diagram represents the current state of the system.

which humanity relies.

Resilience in complex systems is in part a result of the distribution of function within and across the scales of a system (Figure 2). Central to ecological resilience theory is that ecological structures, functions and processes are regulated by a few key variables that operate at characteristic temporal and spatial scales. The potential benefits to understanding resilience for managing systems in the Anthropocene (e.g., predicting regime shifts, assessing effects of humans on ecological resilience) have made quantification of resilience a central pursuit in ecology for decades.

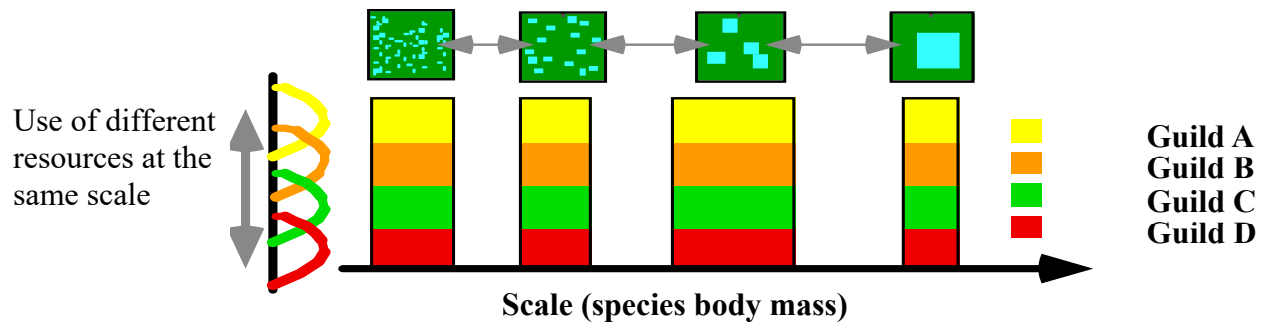


Figure 2. Hypothesized relationship between the scale of a species' interaction with their environment (as assayed by their body size) and their membership in a functional group. Differently-sized species use resources at different spatial and temporal scales. Species in the same functional group use similar resources, but those that operate at larger scales require those resources to be more aggregated in space than do species that operate at smaller scales. Within scales, a diversity of functional groups provides robust ecological functioning, whereas replication of function across scales reinforces ecological function. The combination of a diversity of ecological function at specific scales and the replication of function across a diversity of scales produces resilient ecological function.

Here, we report the final conclusions and implications of our research on developing models to detect ecological regime shifts in space and time, identifying components of adaptive capacity, and identifying species and techniques that may serve as leading indicators of thresholds of changing ecological regimes. This work will enable land managers to create and assess resilience-based frameworks that allows managers to target, and eventually reduce, the uncertainties related to predictability and generalization of vulnerabilities of ecosystems and landscapes to global change.

Objectives

Our chief objectives are to 1) construct conceptual framework for ecosystem-based management that accommodates multiple alternative futures, 2) track ecosystem response to non-stationary conditions by identifying and monitoring appropriate benchmarks of ecosystem status, 3) assess vulnerability using the cross-scale resilience model of ecological community assembly, 4) link this work to regime shift theory to explore potential methods and tools for early detection of non-linear ecosystem responses to non-stationary conditions via management intervention or adaptation, and 5) identify those species traits that are most susceptible to change.

These models will provide means for detecting ecological regime shifts in space and time, identify components of adaptive capacity as relevant to ecological resilience, and identify species, quantitative techniques, and management programs that may serve as leading indicators of thresholds of regime shifts.

Technical Approach

We obtained publicly- available data from the US Geological Survey's North American Breeding Bird Survey. We also obtained proprietary data from natural resource managers at Fort

Riley military base from Fort Riley, KS and remotely-sensed vegetation data from the Rangeland Analysis Platform.

With these data, we developed novel statistical tools and tested existing tools to assess long-term trends in resilience of landscapes, detect and predict ecological regime shifts in both space and time, and identify species vulnerable to decline and extinction, with a focus on the management of Department of Defense properties. We carried out this approach in six tasks:

First, we quantified within-scale and cross-scale aspects of resilience for understanding the capacity of ecosystems to withstand change and avoid shifting to alternate regimes. For instance, cross-scale resilience metrics should be quantifiably different from species richness, cross-scale metrics should constrain species turnover but not variance in turnover, and cross-scale metric patterns should synchronize with abrupt shifts in communities. We tested these predictions by calculating cross-scale resilience model metrics (within-scale redundancy, cross-scale diversity, cross-scale redundancy, number of body mass aggregations) on 46 years of breeding bird data across the United States and testing cross-scale resilience model predictions. We conducted these tests at three different spatial scales per Environmental Protection Agency (EPA) ecoregion Levels II, III, and IV.

Second, we tested methods for detecting broad-scale shifts in regimes across space and time. We used Fisher Information to detect the location of regimes shifts at broad spatial extents, and the occurrence of regime shifts that have occurred over time at specific locations using long-term data available with a spatial and temporal component (e.g., BBS). Fisher Information has been proposed recently as a technique for capturing the dynamic order of ecosystems and detecting dynamic changes in ecological regimes.

Third, we identify discontinuities in species body mass distributions. Discontinuity analysis can provide an objective and independent assessment of scales of structure in a system and can identify early warnings of regime shifts. Using breeding bird presence-absence and body mass data, we performed discontinuity analysis along a 250 km wide and > 3000 km long transect in North America over 46 years to identify shifts in spatial boundaries of regimes and determine if this could be used to detect early warnings of regime shifts on military bases.

Fourth, we identified species with stochastic abundance patterns in space and time. Species with stochastic patterns are hypothesized to be a critical element of resilience in the face of global change, in particular by providing adaptive capacity. We define adaptive capacity as the probability of species to shift from being rare (showing stochastic dynamics) to become dominant and explain deterministic patterns over time in the landscape. We perform this task using distance-based Moran's Eigenvector Mapping, which objectively identifies dominant and stochastic species in space/time. We then compare the richness and diversity of stochastic species to regime boundaries (identified in Task 3) and determine how stochastic species contribute to adaptive capacity in neighboring regimes over time.

Fifth, we detect ecosystem-level shifts and warning indicators within a military installation. In this task, we test the ability of spatial covariance to track spatial regime boundary shifts at Fort Riley. We also test a novel method called "wombling" to track spatial regime boundaries with avian community data collected by Fort Riley personnel.

Military installations are vulnerable to the occurrence of regime shifts at multiple spatial and temporal scales. In this Task we synthesize our multi-faceted approaches to identify and

adapt to (1) regime shifts and vulnerabilities in the matrix surrounding installations and (2) ecosystem-level shifts and vulnerabilities within installations.

Results and Discussion

Task 1

Cross-scale resilience metrics followed patterns predicted by ecological resilience theory: cross-scale resilience metrics did not correlate with species richness; cross-scale resilience metrics constrained the magnitude of species turnover, but they had little effect on the variance of species turnover; and cross-scale resilience metrics both synchronized (cross-scale diversity) and were asynchronous (cross-scale redundancy) with abrupt shifts in community composition. These patterns were mostly consistent across scales of analysis. However, we only observed asynchrony of cross-scale redundancy with abrupt shifts at the middle (EPA Ecoregion Level III) scale.

Our results indicate cross-scale resilience metrics can assess the relative resilience of systems. Thus, using data from a single military installation or multiple within the same ecoregion, cross-scale resilience metrics can be calculated and used to assess the ecological resilience of military bases over time. We show how monitoring changes in these metrics over time can predict when an undesirable regime shift is occurring or about to occur.

Task 2

Interpreting the Fisher Information is currently a qualitative effort. Effective regime detection measures should provide sufficient evidence of the drivers and/or pressures associated with the identified regime shifts. Our findings suggest that Fisher Information is useful for temporal regime shift detection for socioecological data (Eason et al., 2016), but care must be taken when interpreting Fisher Information in spatial contexts and for predictive or management planning purposes. However, Fisher Information is clearly more useful and interpretable—even if only evaluated qualitatively—compared to univariate early warning/regime shift detection methods.

Task 3

Discontinuity analysis revealed three consistent spatial regimes along the south-north transect from 1970 – 2015 (Figure 3a). Tracking these three spatial regime boundaries over 46 years, we found the southernmost spatial regime boundary moved > 260 km northward and the northernmost boundary moved > 590 km northward (Figure 3b). Using discontinuity analysis to track movement of spatial regime boundaries provided > 40 years of early warning of regime shifts. This greatly improves upon traditional early warning methods, which often provide < 1 year of early warning.

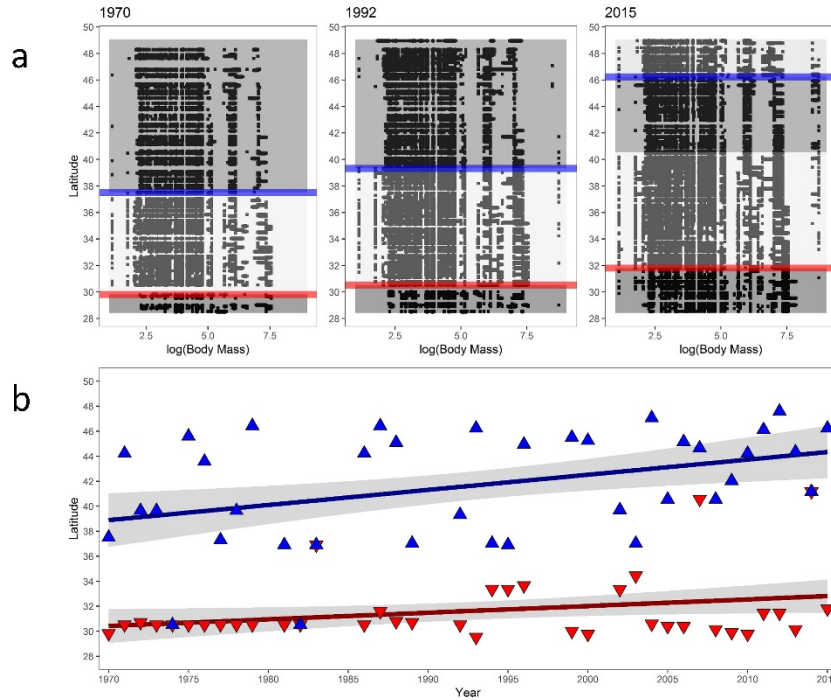


Figure 3. Shifts in spatial regime boundaries demonstrated by breeding bird body mass discontinuities from 1970-2015 in North American Great Plains. **a – b,** (a) Latitudinal spatial regime boundaries (y-axis) determined by log-ranked avian body mass discontinuities (x-axis). Black dots represent body mass aggregations identified via discontinuity analysis in each breeding bird survey route within the transect. Gray-scale boxes represent spatial regimes, and 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, and lines represent modeled northernmost and southernmost spatial regime boundary movement over time with 90% confidence (grey ribbon). When northernmost and southernmost boundaries were the same (i.e., when only one spatial regime boundary was detected in a year), blue and red triangles overlap.

Task 4

Using time series modeling of breeding bird survey data and a space-for-time substitution approach, we found that stochastic species of one regime contribute marginally to within- and cross-scale resilience of a new regime. This refutes our hypothesis that stochastic species may become a critical element of adaptive capacity and resilience after a system has shifted into a new regime. However, we also found the richness and diversity of species with *spatially* stochastic abundance patterns was highest near the spatial centers of spatial regimes (see spatial regimes identified in Task 3).

Task 5

We showed that bird and vegetation spatial regimes corresponded with each other in space and time (Figure 4). The wombling method applied to bird community data responded to tree-grass spatial regime boundaries at Fort Riley Army Base, KS over 27 years (Figure 4). In fact, bird spatial regime boundaries preceded vegetation spatial regime boundaries by > 1 km, suggesting shifts in bird communities may serve as an “earlier” early warning of regime shifts

than vegetation data. Our results indicate that wombling applied to biotic community data can provide spatially-explicit warnings of regime shifts and help military bases prioritize management.

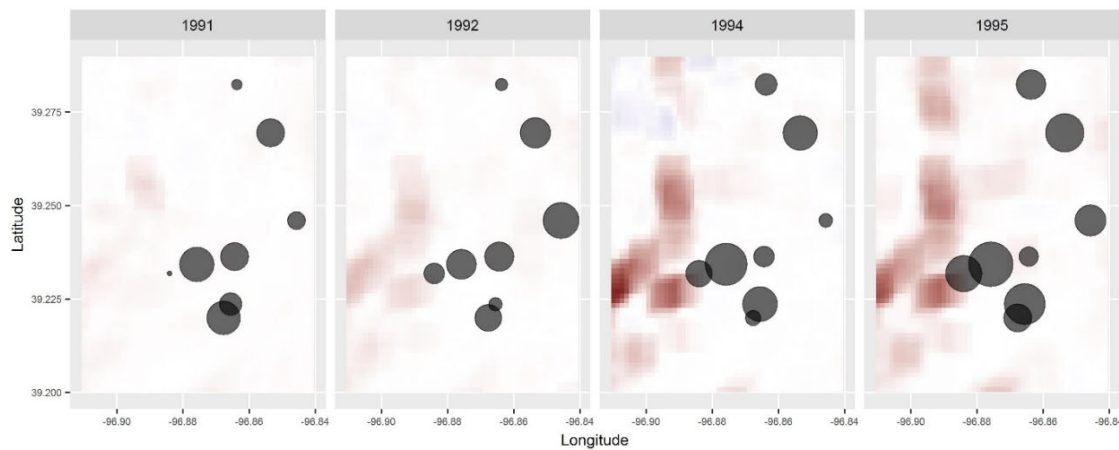


Figure 4. A selected portion of the study area that was likely to exhibit early warnings of changing spatial regime boundaries (regime shifts) due to encroaching tree regimes into grassland regimes. This portion was less disturbed and is near a ravine in which a few trees could have escaped fire and from which tree regimes could expand without fire disturbance. Panels correspond with 4 years in which tree regime boundaries (red shading) rapidly expanded and displaced grassland regimes. Dots indicate bird community sampling locations. Dot size corresponds with wombling (R^2) values, with larger dots indicating greater likelihood of a spatial regime boundary and smaller dots indicating greater similarity lower likelihood of a boundary.

Task 6

In this task, we review and discuss multivariate metrics used to detect early warnings and regime shifts along with their utility in rangeland evaluation and monitoring. We focus on multivariate metrics with potential utility for detecting regime shifts and early warnings, as opposed to univariate indicators, because multivariate methods are more likely to capture the complexity of the systems in question and because comprehensive reviews of univariate metrics already exist that can guide rangeland specialists.

To assist in the appropriate selection and application of multivariate early warning metrics in DoD environmental management, we categorized metrics hierarchically according to their assumptions and data type requirements (Figure 5) and organized the review accordingly. The primary division lies in whether driving state variables are known or unknown for the system in question and whether a relatively small (i.e., limited), or a relatively large (i.e., unlimited) number of state variables have been measured (Figure 5). The second division separates metrics by whether they require the spatial or temporal "location" of a regime shift to be hypothesized *a priori* (Figure 5). The tertiary division splits metrics by specific data type requirements (Figure 5).

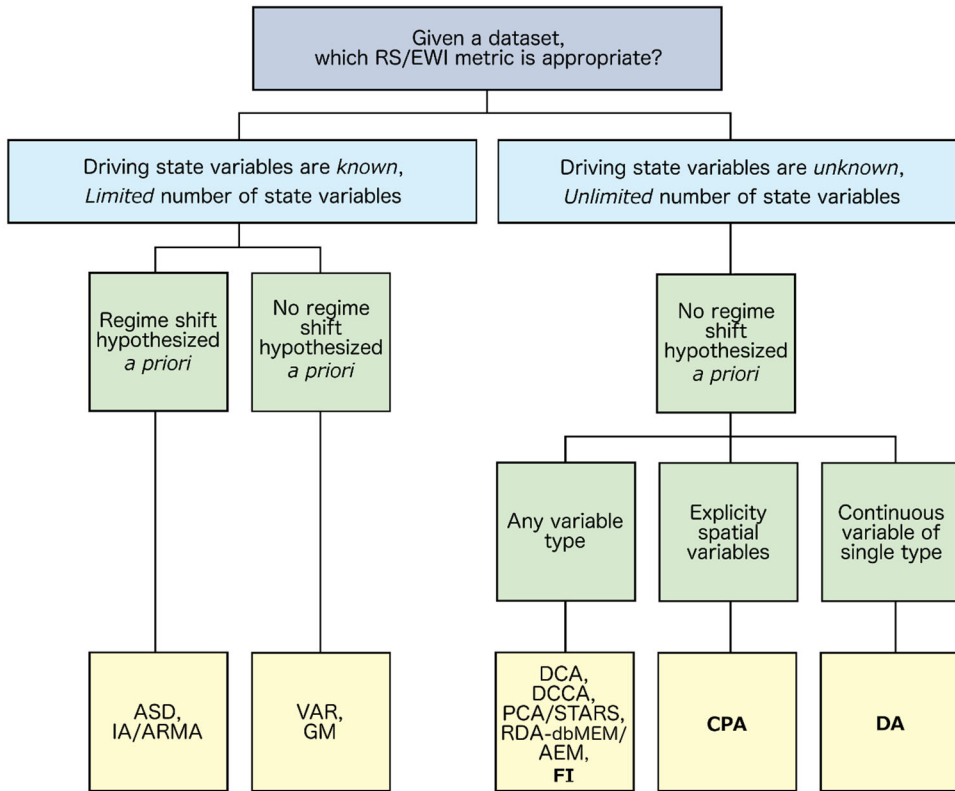


Figure 5. A flowchart for determining which multivariate metrics for regime shift/early warning detection are appropriate for a given set of state variables. “Limited” state variables indicates those metrics are suitable for relatively small number of input variables, and “known drivers” means that the input state variables represent known fundamental influences on system state. The lowest tier lists appropriate metrics for a given data type. Metrics in bold have been tested as early warning indicators of regime shifts. Metrics not in bold have been proposed as early warning metrics but only tested as regime shift indicators. *Note:* RS = proposed early warning indicator, EWI = tested early warning indicator, ASD = Average Standard Deviates, IA/ARMA = Intervention Analysis/Autoregressive Moving Averages, VAR = Vector Autoregression, GM = Generalized Modeling, DCA = Detrended Correspondence Analysis, DCCA = Detrended Canonical Correspondence Analysis, PCA/STARS = Principal Components Analysis/Sequential T-Test Analysis of Regime Shifts, RDA-dbMEM/AEM = Redundancy Analysis- , FI = Fisher Information, CPA = Conditional Probability Analysis, DA = Discontinuity Analysis.

Implications for Future Research and Benefits

Future Research

Future research should center on the identification and detection of scales of regime shifts. Theory suggests regimes should manifest at discontinuous scales. By identifying these ecologically-meaningful scales, the predictive power of our methods may be improved. Here, we have used several scale detection methods (see methods for Task 4) which hold potential, but as yet, they have not been specifically tested for this pursuit.

Benefits

Tracking spatial regime boundaries over time provided decades worth of early warnings of regime shifts along our study transect (Figure 6). This can be interpreted as a “vulnerability assessment” of military bases (Figure 6). That is, if a spatial regime boundary is moving toward a given base, is spatially close to a given base, or both, that base would be considered vulnerable to a regime shift. Thus, by monitoring spatial regime boundary proximity and trajectories over time, military bases can be forewarned of ecological change.

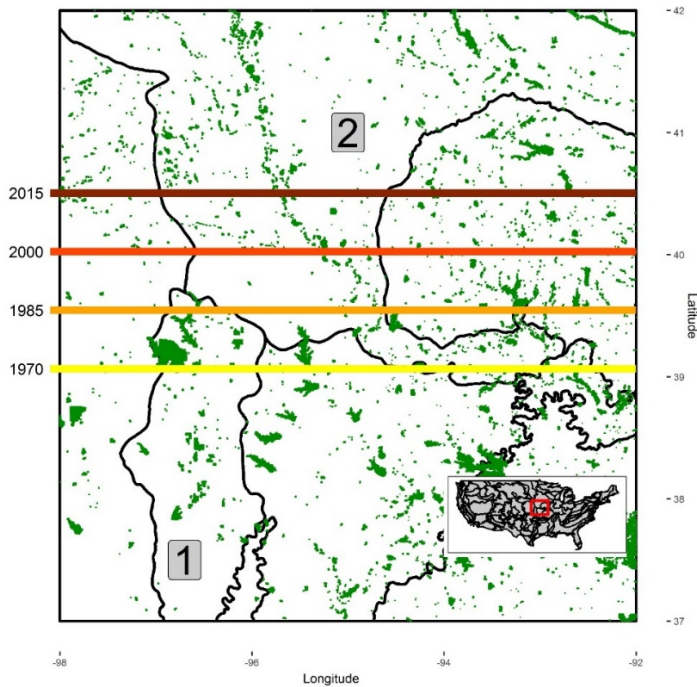


Figure 6. Spatial regime boundary movement between 37 – 42 degrees latitude across a network of protected areas covering in central North America. Black lines indicate level III US Environmental Protection Agency ecoregion boundaries, and green polygons indicate protected areas. The ecoregion labeled No. 1 is the Flint Hills ecoregion, and the ecoregion labeled No. 2 is the Western Corn Belt Plains ecoregion. Predicted spatial regime boundaries (colored horizontal lines) correspond with linear prediction for the years 1970, 1985, 2000, and 2015 ($\beta = 0.032 \pm 0.026$ degrees latitude per year; 90% confidence; $F = 4.093$; $P = 0.052$).

Both individual and a network of military installations stand to benefit from our methods. Tracking spatial regime boundaries over time provides an early warning of regime shifts for both individual bases and for a network of bases in the path of the regime shift. While a single base may not be able to halt or overcome a continental-scale regime shift, a network of bases, working in tandem, working with other land management agencies, and forewarned by spatial regime monitoring may have a chance to avert such a broad-scale shift. However, individual bases, employing spatial and temporal regime shift detection methods within their borders, also can benefit from the early warning signals: these signals, particularly spatial methods such as wombling, can help base managers pinpoint where change is occurring within their bases and more efficiently prioritize restoration, management, etc. in those areas.

OBJECTIVES

The primary objectives of SON RCSON15-01 RC-2510 “Global Change, Vulnerability, and Resilience: Management Options for an Uncertain Future”. Our chief aims are to 1) construct conceptual framework for ecosystem-based management that accommodates multiple alternative futures, 2) track ecosystem response to non-stationary conditions by identifying and monitoring appropriate benchmarks of ecosystem status, 3) assess vulnerability using the cross-scale resilience model of ecological community assembly, 4) link this work to regime shift theory to explore potential methods and tools for early detection of non-linear ecosystem responses to non-stationary conditions via management intervention or adaptation, and 5) identify those species traits that are most susceptible to change. This project addressed the following tasks:

Task 1. Quantify within-scale and cross-scale aspects of resilience for understanding the capacity of ecosystems to withstand change and avoid shifting to alternate regimes.

Task 2. Detect broad-scale shifts in regimes across space and time.

Task 3. Identify discontinuities in species body mass distributions to provide an objective and independent assessment of scales of structure in a system and identify the usefulness of fluctuations in the abundance of an indicator species for monitoring early warnings of regime shifts.

Task 4. Identify species with stochastic abundance patterns in space and time. Species with stochastic patterns are hypothesized to be a critical element of resilience in the face of global change, in particular by providing the ability to maintain critical functions after disturbances in systems.

Task 5. Detect ecosystem-level shifts and warning indicators within a military installation.

Task 6. Synthesize our approaches and provide examples of how to identify regime shifts and vulnerabilities in the matrix surrounding installations and identify vulnerabilities within installations.

The approaches described herein will provide means for detecting ecological regime shifts in space and time, identify components of adaptive capacity as relevant to ecological resilience, and identify species, quantitative techniques, and management programs that may serve as leading indicators of thresholds of regime shifts.

BACKGROUND

Globally, environmental change is on the rise, and the ecological resilience of many ecosystems is eroding. This is leading to increases in regime shifts, where fundamental structures and functions of ecosystems change. Loss of resilience and regime shifts can strongly affect human well-being and military installation readiness via alteration or loss of ecosystem services such as decreases in threatened and endangered species populations, species that were once abundant becoming threatened, and loss of ideal military training landscapes (e.g., grassland at Fort Riley, Kansas, pine savannas and swamps at Eglin Air Force Base, Florida).

Ecological resilience theory and the allied complexity theory arose to attempt to describe and predict changes and behaviors of so-called complex adaptive systems—which ecosystems are counted as (Holling, 1973; Levin, 1998). These theories provided frameworks to account for and predict uncertainty, complexity, and non-stationarity in ecological systems. Broadly, resilience theory acknowledges that ecosystems are not static, that multiple alternative ecosystem states exist, and that the resilience of a system is an emergent attribute that determines how much disturbance the system can absorb before shifting into an alternate state (i.e., a regime shift) (Holling, 1973). That is, resilience theory predicts ecosystems do not have an equilibrium state, where opposing forces are in balance, as assumed by an engineering definition of resilience. An ecosystem exists within a regime, a set of structuring processes interacting with biotic and abiotic components that are compartmentalized by scale in the system. Within a particular regime, the abundance and composition of the species that constitute that regime may change quite dynamically over time.

Similarly, complexity theory assumes that the properties of a system are greater than the simple sum of its parts (meaning systems have emergent properties), that complex adaptive systems self-organize and exhibit self-similarity (hallmarks of ecosystems), perfect knowledge of system behavior cannot be attained, and uncertainty must therefore be embraced (Levin, 1998). Together, resilience and complexity theory provide a foundation for grappling with non-stationarity and for securing the goods and services ecosystems provide humanity.

Spawned from resilience and complexity theories, ecology has now begun pursuing tools capable of predicting ecosystem vulnerability to regime shifts, metrics for quantifying ecological resilience, and assessing how our current natural resource management policies foster or erode resilience (Angeler & Allen, 2016; Scheffer et al., 2009; Twidwell, Allred, & Fuhlendorf, 2013). For example, the search for early warnings of regime shifts has exploded in the past two decades (Clements & Ozgul, 2018; Dakos, Carpenter, Nes, & Scheffer, 2015). Early warning indicators seek to detect signals of impending regime shifts in ecosystems and thereby provide managers and policymakers time to take action and “turn back from the brink” (Biggs, Carpenter, & Brock, 2009; Roberts et al., 2018). Additionally, quantifying resilience has progressed from using subjective “resilience surrogates” to estimate resilience to metrics that more directly represent the cross-scale structure and function of ecosystems (Allen, Gunderson, & Johnson, 2005; Bennett, Cumming, & Peterson, 2005). For example, resilience theory predicts resilience increases with an increased diversity and redundancy of ecological function among species of different functional groups that operate across scales (Allen et al. 2005). These metrics are meant to enable tracking of resilience over time and space and determine how disturbances and

management affect system resilience (Sundstrom et al., 2018; Roberts et al., 2019b). And finally, models of complex system behaviors such as models of invasive species impacts and models of ecological vulnerability have been developed to promote efficient, scientifically-based strategies for managing non-stationary natural resources (Yokomizo, Possingham, Thomas, & Buckley, 2009).

Here, we synthesize these theories and tools to develop novel methodologies and strategies for managing ecosystems in a non-stationary world. The structure of this report begins with a review of the current state of resilience and complexity-based tools in natural resources management (e.g., rangelands) and a synthesis of promising new concepts and methods. It then moves to several studies operationalizing and investigating individual tools and methods. The ability to quantify ecosystem resilience and detect early warnings of regime shifts would allow land managers, land owners, and policymakers to make informed decisions, appropriate conservation efforts, and take adaptive measures in the midst of ecological change and uncertainty.

Task 1. Quantify within-scale and cross-scale aspects of resilience

As the Anthropocene progresses, community change and collapse are increasingly common (Folke et al., 2004; Steffen et al., 2015). The concept of ecological resilience, defined by C. S. Holling (1973) as the amount of disturbance a system can absorb before collapsing into an alternative regime, holds potential for predicting community change and collapse (Angeler & Allen, 2016). Quantifying ecological resilience has been a long-term pursuit in ecology (Carpenter, Westley, & Turner, 2005; Cumming et al., 2005; Standish et al., 2014), ecological resilience has been applied internationally in management frameworks (Briske et al., 2008; Bestlemeyer et al., 2017; Seidl et al., 2016), and multiple ecological resilience metrics have been proposed (Allen et al., 2005; Baho et al., 2017). Yet neither the core predictions nor metrics of ecological resilience theory have received rigorous testing (Angeler and Allen, 2016; Sundstrom et al., 2018).

Ecological resilience theory makes key predictions concerning complex, nonlinear, and abruptly shifting system behavior, making it uniquely applicable to Anthropocene issues (L. H. Gunderson, 2000). Ecological resilience is related to, but distinct from, ecological stability (the ability of a system to return to an equilibrium state post-disturbance—also known as “engineering resilience,” “bounce-back time,” “resistance,” and “elasticity”; C. S. Holling, 1973; Hillebrand et al., 2018; Pimm, 1984). This is a crucial distinction because while ecological resilience makes predictions concerning abrupt regime shifts into alternative states, ecological stability only makes predictions concerning a single regime (Angeler and Allen, 2016). Ecological resilience theory predicts that a system may fluctuate greatly (have low stability and exhibit non-equilibrium behavior) and yet have high ecological resilience or conversely fluctuate little and have low ecological resilience (Angeler & Allen, 2016; C. S. Holling, 1973). That is, a resilient system will constrain the magnitude of fluctuations so that the system stays within a given regime, but the same resilient system may exhibit high instability within the regime (L. H. Gunderson, Allen, & Holling, 2012). By definition, loss of ecological resilience increases the likelihood of system collapse and regime shifts due to loss of structures, functions, and feedbacks that maintain the current regime (Allen, Gunderson, & Johnson, 2005). Thus, ecological resilience should be both quantifiably distinct from stability and clearly correspond with community change and collapse (C. S. Holling, 1973; Standish et al., 2014).

The cross-scale resilience model, a leading model for operationalizing and quantifying ecological resilience (hereafter referred to simply as “resilience”), provides the opportunity to test these core predictions of resilience theory (G. Peterson et al., 1998; S. M. Sundstrom et al., 2018). The cross-scale resilience model establishes that redundancy and diversity of organism functions across discontinuous scale domains of resource use in a system confer resilience (C. S. Holling, 1992; G. Peterson et al., 1998; Figure 1). Quantifying redundancy and diversity of functions across these discontinuous scale domains can produce metrics to estimate the relative resilience of systems (Bouska, 2018; Sundstrom et al., 2018; Angeler et al., 2019a). For example, Allen et al. (2005) proposed several cross-scale resilience metrics such as within-scale redundancy, cross-scale redundancy, cross-scale diversity, and number of scale domains.

Here, we use a half-century of sub-continental avian community data to calculate cross-scale resilience metrics and test how resilience relates to community stability and collapse. We do this by testing two core resilience theory predictions concerning its relationship with stability and two concerning its relationship with community change and collapse. The first resilience-stability relationship prediction is that resilience is distinct from stability: we test this by

quantifying the degree of correlation between species richness and cross-scale resilience metrics. Although species richness is not a direct metric of stability, it is correlated with stability and influences the ability of a system to “bounce back” from disturbances (Hautier et al., 2015; Ives & Carpenter, 2007; McCann, 2000; Mougi & Kondoh, 2012; Tilman & Downing, 1994). The second resilience-stability relationship prediction is that resilience will constrain the magnitude of system fluctuations but not their variability: we test this by determining the relationship between cross-scale resilience metrics and the mean and variance of annual species turnover. In this case, cross-scale diversity is expected to reduce mean turnover the most, and all resilience metrics should have little influence on turnover variance (Allen et al., 2005; Angeler et al., 2019a). The first resilience-collapse relationship prediction is that changes in cross-scale resilience metrics will predict community collapse: we test this by determining if changes in cross-scale resilience metrics synchronize with abrupt shifts in community composition. Within-scale redundancy, cross-scale redundancy, and number of scale domains are expected to most strongly predict community collapse (Nash et al., 2016; Roberts et al., 2019; Spanbauer et al., 2016). Finally, the second resilience-collapse prediction is cross-scale resilience metrics will only weakly predict maintenance of specific species assemblages: we test this by determining how cross-scale resilience metrics relate to changes in community similarity over time (L. H. Gunderson, 2000; Angeler et al., 2019b).

Materials and Methods

Calculating cross-scale resilience metrics

Cross-scale resilience metrics are calculated by first identifying a biotic community within a system (e.g., an avian forest community) and acquiring census presence/absence data from the biotic community (Allen et al., 2005), identifying the discontinuous scale domains at which functions are performed by each species in the biotic community (Nash et al., 2014a, b), and finally using functional traits of species across scale domains to estimate functional redundancy and diversity within and across scale domains (Fischer et al., 2007).

Identifying biotic communities

For biotic community data, we used the North American Breeding Bird Survey (BBS) which estimates bird community composition via yearly roadside avian point-count surveys (Sauer et al., 2013). Begun in 1966, the BBS is conducted along a series of > 2500 permanent, randomly-distributed routes during the breeding season (Sauer et al., 2013). We analyzed BBS route data from 1967 - 2014.

We defined avian communities by spatially binning BBS routes according to US Environmental Protection Agency (EPA) ecoregions (Omernik & Griffith, 2014; Figure 2). These ecoregions are spatially hierarchical, meaning that finer-scaled ecoregions are bounded by and nested within larger-scaled ecoregions. Because smaller-scale EPA ecoregion boundaries are bounded by US political boundaries, we only consider BBS routes within the continental United States. We considered avian communities at the three progressively smaller spatial scales (EPA ecoregion levels II, III, IV; Figure 2). If binned BBS data within an ecoregion did not extend for

≥ 24 years (i.e., $\geq 50\%$ of the study period), we excluded that ecoregion from analysis (Table S1; see supplementary computer code for further details).

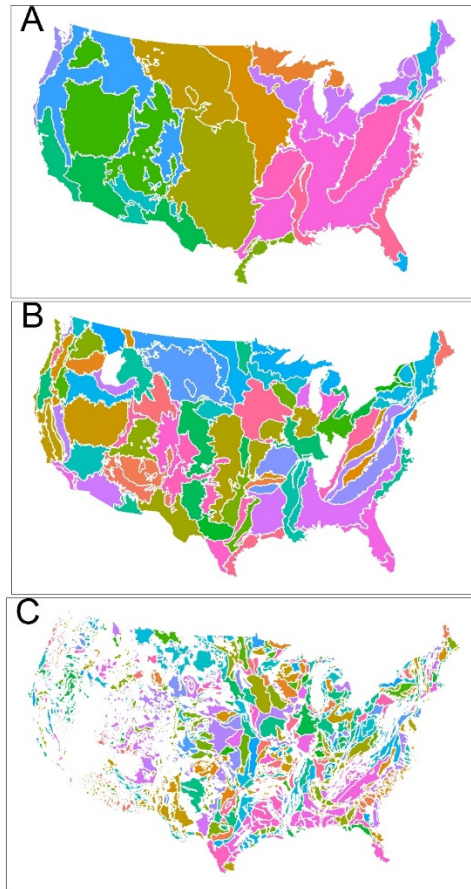


Figure 7. Maps of US Environmental Protection Agency ecoregions corresponding with level 2 (A), level 3 (B), and level 4 (C). Missing (white-out) ecoregions did not contain sufficiently long time series of North American Breeding Bird Survey data (≥ 24 years). White lines indicate ecoregion boundaries.

Identifying discontinuous scale domains

We performed discontinuity analysis on binned BBS data for each ecoregion at each scale using the “discontinuity detector” method (Barichievy et al., 2018) based on the Gap Rarity Index which identifies scale domains by detecting discontinuities in log-ranked organism body masses (Restrepo et al., 1997). For taxa with determinant growth, mean body mass reliably differentiates size aggregations and is strongly allometric to the scale domains at which functions are carried out by organisms (Allen et al., 2006; C. S. Holling, 1992; Nash et al., 2014b). Because of known negative observation biases for waterfowl and allied families and because water-dwelling avian families’ follow different body masses 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 (C. S. Holling, 1992; S. M. Sundstrom, Allen, & Barichievy, 2012). We obtained mean body mass estimates for all remaining species from the CRC Handbook of Avian Body Masses (Dunning Jr, 2007). Because Gap Rarity Index tends to overestimate discontinuities in species-poor samples, we removed any route with < 40 species observed (Barichievy et al., 2018; Stow, Allen, & Garmestani, 2007). We simply counted the number of body mass aggregations to obtain that metric.

Estimating within- and cross-scale functional redundancy, cross-scale diversity

We assigned functional types to each species according to diet and foraging strategies (Ehrlich, Dobkin, & Wheye, 1988). We broke diets into carnivore, herbivore, and omnivore groups, where omnivores are defined as species with approximately even proportions of plant and animal intake (Bouska, 2018). We divided foraging strategies into five groups: water, ground, foliage, bark, and air (S. M. Sundstrom et al., 2012). Thus, functional groups represented combinations of diet and foraging strategies (e.g., water carnivore, ground herbivore, etc.). We then used functional groups along with body mass aggregations to calculate cross-scale redundancy (average number of aggregations for which each functional group has at least one representative), within-scale redundancy (the average number of representatives from each functional group within each aggregation), and cross-scale diversity (the average diversity of functional groups across aggregations) metrics for each ecoregion within each of the three spatial scales (Figure 2). The equations for these are as follows:

$$\text{Cross – scale Redundancy} = \frac{1}{a} \sum_{i=1}^a (\varphi)_i$$

$$\text{Within – scale Redundancy} = \frac{1}{a} \sum_{i=1}^a \left(\frac{1}{f} \sum_{j=1}^f f_j \right)_i$$

$$Cross - scale Diversity = \frac{1}{a} \sum_{i=1}^a \left(- \sum_{j=1}^f p_j \ln p_j \right)_i$$

Where a is the number of body mass aggregations, ϕ is the number of functional groups with at least one representative in an aggregation, f is the j th functional group, and p is the j th species in each aggregation.

Resilience-Stability Test 1: Relationship between cross-scale resilience and richness

We used cross-correlation to compare species richness with each cross-scale resilience metric (number of body mass aggregations, cross-scale redundancy, within-scale redundancy, cross-scale diversity) for each ecoregion across -5 to 5 lags. That is, we used cross-correlation to quantify temporal covariance of richness and resilience metrics, determining if patterns of resilience metrics preceded (back to 5 time steps before) or followed (forward to 5 time steps after) patterns of richness. For each lag, we calculated the mean and 85% confidence intervals of the absolute values of correlation coefficients across ecoregions.

Resilience-Stability Test 2: Relationship between cross-scale resilience and turnover

Second, we determined the relationship between cross-scale resilience metrics and species turnover. We calculated relative species turnover (the proportion of the species pool that turns over annually) using the following equation (Diamond, 1969; Wonkka, West, Twidwell, & Rogers, 2017):

$$Turnover_{t+1} = (U_t + U_{t+1}) / (S_t + S_{t+1})$$

where U_t is the number of species present in the ecoregion at year t that were not present in year $t + 1$; U_{t+1} is the number of species present in the ecoregion at year $t+1$ that were not present in year t ; S_t is the total number of species present in the ecoregion at year t ; and S_{t+1} is the total number of species present in the ecoregion at year $t + 1$.

We then developed two linear mixed models: 1) to determine if resilience metrics influenced the magnitude of species turnover, we used the mean of the absolute value of species turnover over time as the response variable, and 2) to determine if resilience metrics influenced the variability of species turnover, we used the standard deviation of species turnover over time as the response variable. For both models, we set mean resilience metrics over time as the predictor variables.

We allowed intercepts to vary by hierarchically nested EPA ecoregions (e.g., for level III ecoregions, random effect in R package “lme4” syntax was “(1 | Level I / Level II)”). To minimize collinearity, we calculated variance inflation factors and sequentially removed

predictor variables (resilience metrics) with the highest variance inflation factor until variance inflation factor values for all variables were ≤ 3 .

Resilience-Collapse Test 1: Relationship between cross-scale resilience and abrupt shifts

We determined whether significant temporal shifts in cross-scale resilience metrics synchronized with abrupt shifts in community composition. To identify abrupt shifts in community composition, we 1) performed detrended correspondence analysis (DCA; “decorana” function from the vegan package in R) on Hellinger-transformed relative abundances of species in each ecoregion over time, 2) extracted values of the first DCA axis (DCA1) for each year, 3) used generalized additive models (GAMs) to model changes in DCA1 over time (with year as the smoothed predictor) for each ecoregion, 4) extracted predicted DCA1 response values from GAMs for each ecoregion (Figure 3a), and 5) determined where community structure significantly changed by first calculating derivatives and 85% confidence limits around the derivatives from the GAM predictions and then locating ranges in the time series where derivative confidence limits did not encompass zero (Simpson, 2018; Figure 3b). We located shifts in cross-scale resilience metrics in a similar fashion—by extracting GAM predictions, calculating derivatives and confidence intervals, and locating ranges where confidence limits did not encompass zero (Figure 3b). To test for synchrony between cross-scale resilience metrics and structural community change, we encoded DCA1 and resilience metric time series as binary variables, where either a significant shift (85% confidence limit of derivative did not encompass zero) occurred or did not for each time step (i.e., each year of BBS data; Figure 3c). We aggregated significant increases and decreases into an absolute value because both significant increases and decreases in ordinated values (e.g., DCA) or resilience metrics, regardless of directionality, could signal regime shifts. We set the binary DCA1 variable as the response and binary resilience metrics predictors in a binomial generalized linear mixed model. We checked for collinearity with variance inflation factors.

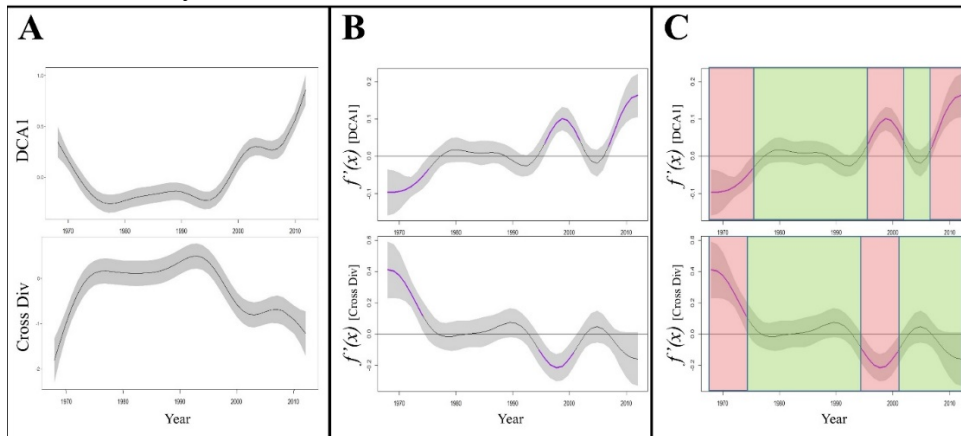


Figure 8. Visual depiction of methods for detecting synchrony/asynchrony in abrupt shifts in community composition (DCA1) and in resilience metrics (e.g., cross-scale diversity [Cross Div]). Panel A shows an example of predicted DCA1 and Cross Div values derived from generalized additive models. Panel B shows approximate derivatives of predicted DCA1 and Cross Div values. Panel C shows the binary test for synchrony/asynchrony, where red bars (abrupt shifts) and green bars (no abrupt shift detected) aligning indicate synchrony and lack of alignment indicates asynchrony.

Resilience-Collapse Test 2: Relationship between cross-scale resilience and community similarity

We determined the relationship between cross-scale resilience metrics and patterns of community similarity over time. We estimated community similarity over time via the Jaccard index. That is, we calculated Jaccard similarity between each year of BBS data for each ecoregion and then used linear regression to estimate change in community identity over time (i.e., slope; *sensu* Dornelas et al., 2014). Because the Jaccard index ranges from 0 (complete dissimilarity in species) to 1 (complete similarity in species), a slope of zero indicates no change in community composition over time, and a slope of -1 indicates a complete change in species pool. We then developed linear mixed models, setting the slope of the Jaccard index as the response variable. For predictor variables, we used initial resilience metric values (the chronologically first value for each resilience metric for each ecoregion) and mean resilience metric values (the average of each resilience metric value across the time series for each ecoregion). To account for variance in certainty of Jaccard slope fits, we used $1 / \text{standard error}$ of each Jaccard slope fit as prior weights for linear mixed models. We used the methods from Test 2 for minimizing collinearity as above (i.e., sequential removal of predictor variables via variance inflation factors).

Results and Discussion

Results

Resilience-Stability Test 1: Relationship between cross-scale resilience and richness

Mean cross-correlation between richness and resilience metrics was low across scales and individual metrics, ranging from $r = 0.16 \pm 0.01$ (cross-scale redundancy at lag -5 at the finest scale) to $r = 0.63 \pm 0.02$ (cross-scale diversity at lag 0 at the finest scale; Figure 9). Patterns were consistent across scales: the strongest correlation between richness and all metrics at all scales occurred at lag zero (annually) after which correlations decreased sharply (Figure 9). At the broadest scale (level II), confidence limits show little difference between individual metrics' correlations with richness (Figure 9). At the finer scales (levels III, IV), cross-scale diversity correlated most strongly with richness (Figure 9). Within-scale redundancy showed the second greatest correlation with richness (max $r = 0.50 \pm 0.02$ at level IV, lag 0; Figure 9). Cross-scale redundancy ($r = 0.34 \pm 0.02$ at lag 0) and number of aggregations (0.29 ± 0.02 at lag 0) displayed the weakest correlation with richness at finer scales (Figure 9).

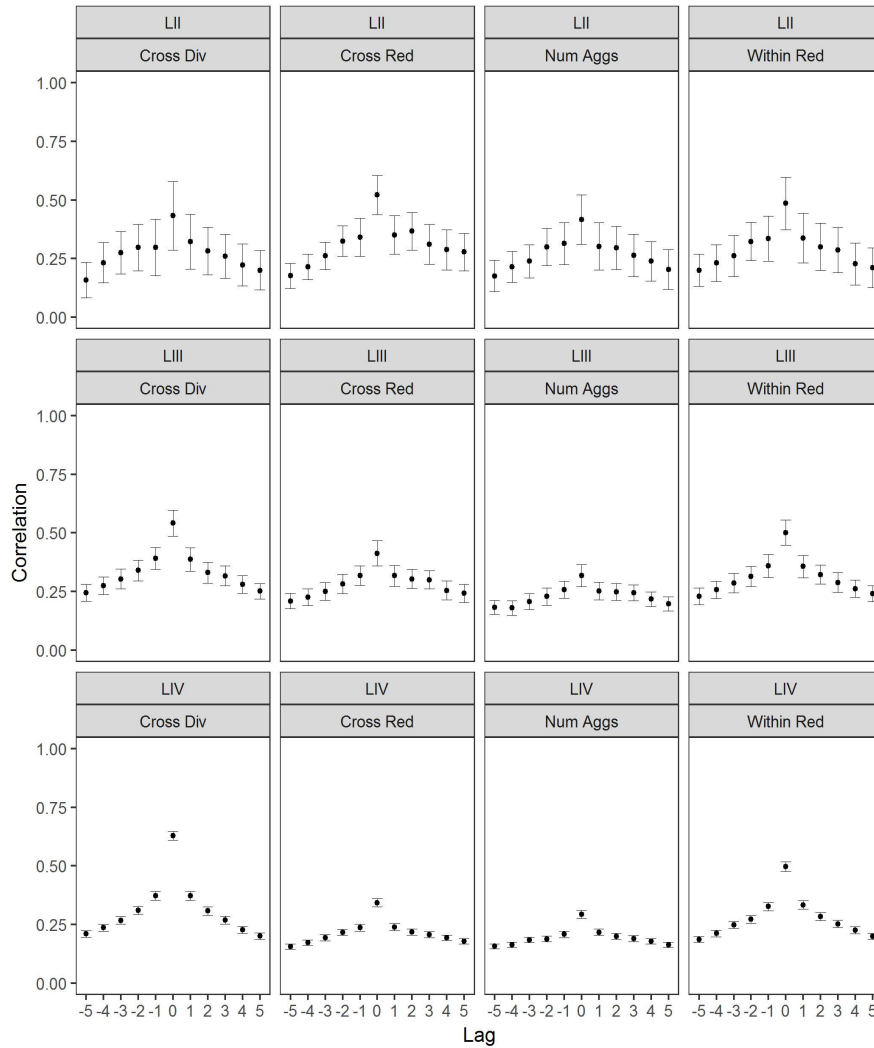


Figure 9. Mean cross-correlation estimates and 85% confidence limits between species richness and cross-scale resilience metrics at multiple hierarchical scales. Y-axis indicates degree of correlation (r), and x-axis indicates lags ranging from -5 to 5, where lag 0 indicates annual correlation. Richness and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1967 - 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.

Resilience-Stability Test 2: Relationship between cross-scale resilience and turnover

Resilience metrics had significantly negative relationships with mean annual species turnover at all scales, but resilience metrics showed little or no association with standard deviation of annual species turnover (Figure 10; Table 1). Cross-scale diversity was a significant predictor of mean species turnover at the broadest scale and the strongest predictor at the finest scale (-0.027 ± 0.001 and -0.034 ± 0.002 at levels II and IV respectively), and cross-scale diversity was a significant negative predictor of standard deviation in species turnover at the

finest scale (-0.004 ± 0.002). Cross-scale redundancy was a significant predictor at all scales, although its strength decreased at finer scales until it was the weakest predictor at the finest scale (-0.018 ± 0.011 , -0.015 ± 0.001 , and -0.0059 ± 0.004 at ecoregion levels II, III, and IV respectively). Cross-scale redundancy also significantly negatively predicted standard deviation in species turnover at the finest scale (-0.005 ± 0.003). Within-scale redundancy was a significant predictor at the middle scale (-0.017 ± 0.006), and number of aggregations was a significant predictor of middling strength at the finest scale (-0.018 ± 0.004).

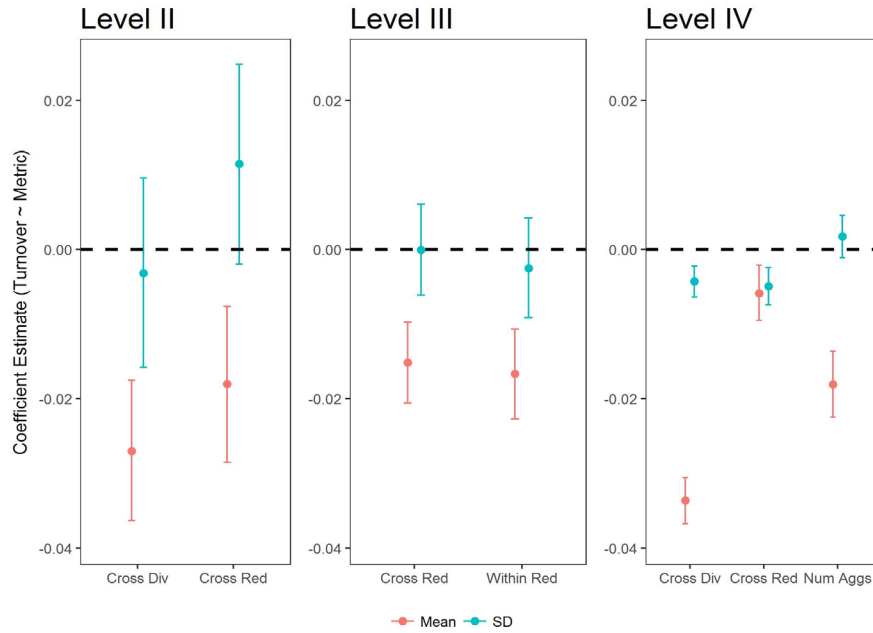


Figure 10. Coefficient estimates and 85% confidence limits from linear mixed models testing the relationship between mean annual species turnover and mean resilience metrics (red dots) and the standard deviation (SD) of annual species turnover and mean resilience metrics (blue dots) at multiple hierarchical scales. Species turnover and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1967 - 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). *Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.*

Table 1. Results from linear mixed models testing the relationship between mean annual species turnover and mean resilience metrics (Response = Mean) and the standard deviation (Response = SD) of annual species turnover and mean resilience metrics at multiple hierarchical scales. Species turnover and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1966 - 2014 aggregated by US Environmental Protection Agency ecoregions. Columns indicate ecoregion level, response type, variable name, coefficient estimate, standard error of coefficient estimate, and t-value estimate for coefficient.

Ecoregion Level	Response	Variable	Estimate	SE	t-value
LII	Mean	Intercept	0.079	0.0092	8.5
LII	Mean	Cross-scale Redundancy	-0.018	0.0073	-2.5

LII	Mean	Cross-scale Diversity	-0.027	0.0065	-4.1
LIII	Mean	Intercept	0.11	0.0077	14
LIII	Mean	Within-scale Redundancy	-0.017	0.0042	-4
LIII	Mean	Cross-scale Redundancy	-0.015	0.0037	-4.1
LIV	Mean	Intercept	0.15	0.0056	26
LIV	Mean	Cross-scale Redundancy	-0.0059	0.0026	-2.3
LIV	Mean	Number of Aggregations	-0.018	0.003	-5.9
LIV	Mean	Cross-scale Diversity	-0.034	0.0021	-16
LII	SD	Intercept	0.053	0.015	3.4
LII	SD	Cross-scale Redundancy	0.011	0.0093	1.2
LII	SD	Cross-scale Diversity	-0.0032	0.0088	-0.36
LIII	SD	Intercept	0.046	0.0058	8
LIII	SD	Within-scale Redundancy	-0.0025	0.0047	-0.54
LIII	SD	Cross-scale Redundancy	-4.00E-05	0.0042	-0.0086
LIV	SD	Intercept	0.052	0.0037	14
LIV	SD	Cross-scale Redundancy	-0.0049	0.0017	-2.8
LIV	SD	Number of Aggregations	0.0017	0.002	0.88
LIV	SD	Cross-scale Diversity	-0.0043	0.0014	-3

Table 2. Results from linear mixed models testing the relationship between community compositional change over time (slope of Jaccard index over time) and initial and mean resilience metrics at multiple hierarchical scales. Jaccard index and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1966 - 2014 aggregated by US Environmental Protection Agency ecoregions. Columns indicate ecoregion level, variable name, coefficient estimate, standard error of coefficient estimate, and t-value estimate for coefficient.

Ecoregion Level	Variable	Estimate	SE	t-value
LII	Intercept	-0.0019	0.00039	-4.8
LII	Within Red Initial	-0.00043	0.00094	-0.46
LII	Cross Red Mean	3.00E-05	0.00038	0.092
LII	Cross Red Initial	-7.00E-05	0.00042	-0.16
LIII	Intercept	-0.0021	0.00015	-14
LIII	Within Red Mean	-0.00014	0.00021	-0.66
LIII	Cross Red Mean	0.00018	0.00021	0.86
LIII	Cross Red Initial	0.00015	0.00016	0.93
LIII	Cross Div Initial	0.00014	0.00012	1.2
LIV	Intercept	-0.0022	0.00015	-14
LIV	Num Aggs Mean	-1.00E-05	0.00015	-0.064
LIV	Num Aggs Initial	0.00016	1.00E-04	1.5
LIV	Cross Red Mean	0	0.00015	0.029
LIV	Cross Red Initial	-4.00E-05	9.80E-05	-0.45
LIV	Cross Div Initial	0.00024	8.60E-05	2.8

Notes: *Within Red Initial* = Within-scale Redundancy initial metric value; *Cross Red Mean* = Cross-scale Redundancy mean metric value; *Cross Red Initial* = Cross-scale Redundancy initial metric value; *Within Red Mean* = Within-scale Redundancy mean metric value; *Cross Div Initial* = Within-scale Diversity initial metric value; *Num Aggs Mean* = Number of Body Mass Aggregation mean value; *Num Aggs Initial* = Number of Body Mass Aggregation initial value.

Resilience-Collapse Test 1: Relationship between cross-scale resilience and abrupt shifts

At all scales, resilience metrics synchronized significantly with abrupt community shifts (Figures 11, 12; Table 3). At the broadest scale (level II), cross-scale diversity (1.0 ± 0.53) and cross-scale redundancy (0.67 ± 0.55) synchronized with community change (Figure 4). At the middle scale (level III), number of aggregations (0.21 ± 0.20) and within-scale redundancy (0.62 ± 0.20) exhibited synchrony with community change (Figure 3), but cross-scale redundancy exhibited asynchrony (i.e., a negative model coefficient; -0.3 ± 0.19) with community change (Figures 11, 12). And at the finest scale (level IV), all resilience metrics synchronized with

abrupt community shifts: cross-scale diversity showed the strongest synchrony (0.58 ± 0.08 ; Figure 11), and number of aggregations showed the weakest synchrony (0.11 ± 0.09).

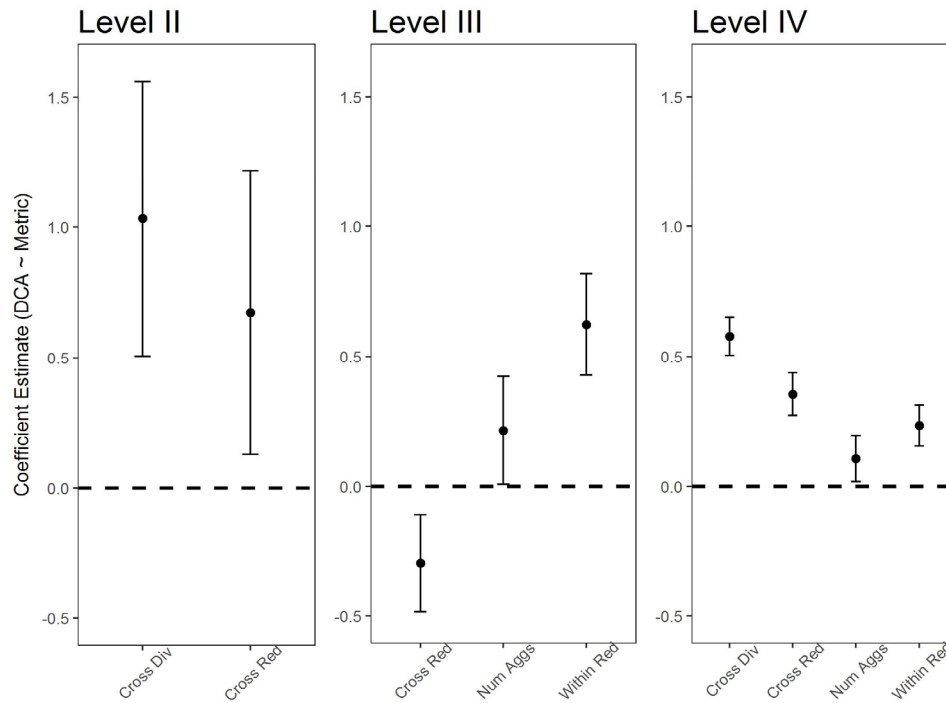


Figure 11. Coefficient estimates and 85% confidence limits from binomial generalized linear mixed models testing synchrony between abrupt community shifts and resilience metrics at multiple hierarchical scales. Synchrony is defined as simultaneous occurrence of regime shifts (i.e., significant change in first axis of Detrended Correspondence Analysis) and significant shifts in resilience metrics. Abrupt community shifts and resilience metrics were derived from avian community data recorded at North American Breeding Bird Survey routes from 1967 - 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). *Note: DCA = first axis of detrended correspondence analysis; Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.*

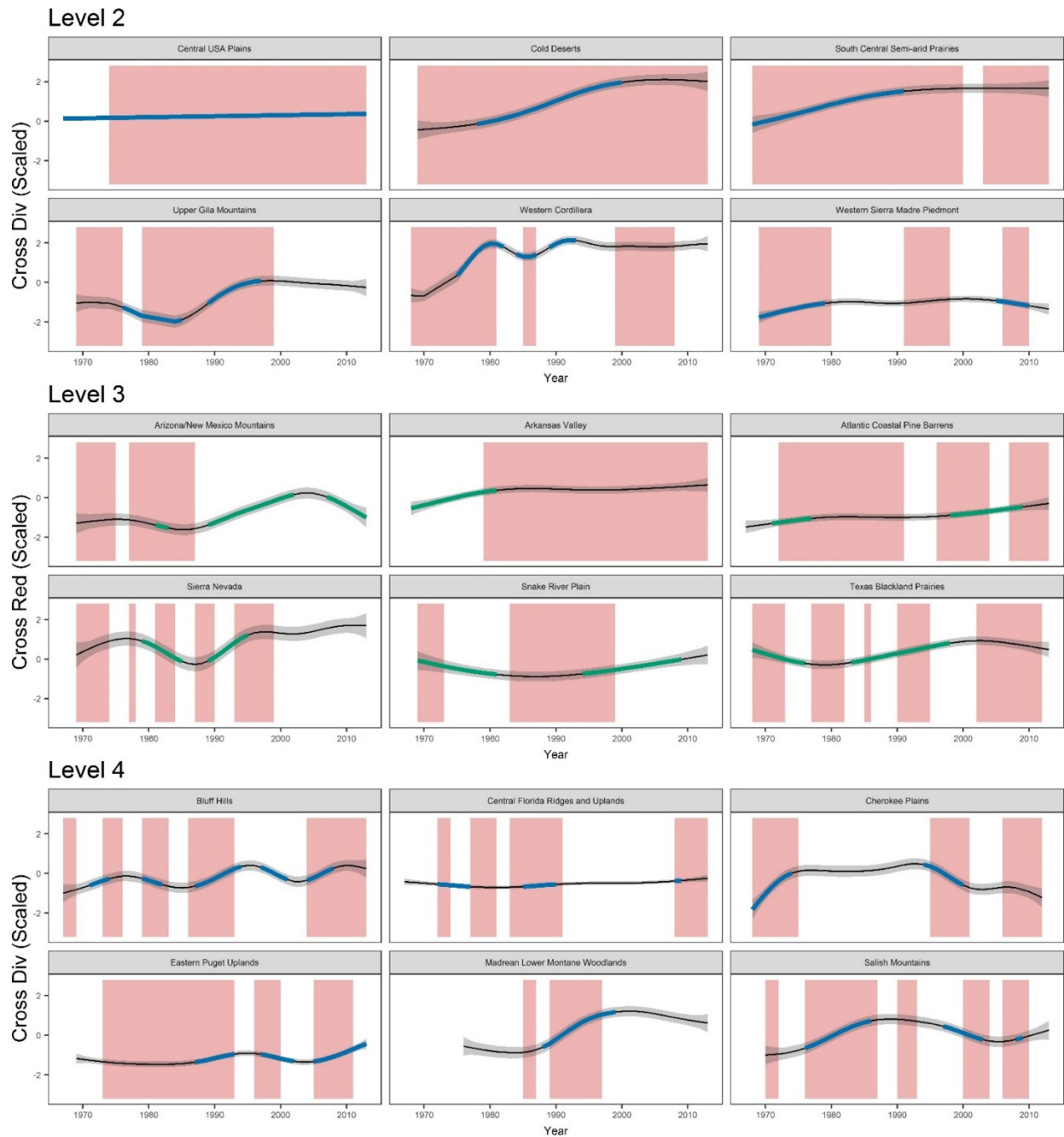


Figure 12. Comparison of synchrony/asynchrony between periods of significant avian abrupt community shifts (red blocks) and periods of significant changes in cross-scale resilience metrics across a sample of Environmental Protection Agency Levels 2, 3, and 4 ecoregions from 1967 - 2014. Black lines (y-axis) indicate predicted values from GAMs of resilience metrics, grey shading indicates pointwise 85% confidence limits around predictions, and colored sections indicate regions of significant change in time series (where simulated confidence limits of derivatives from GAMs did not encompass zero). *Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy.*

Table 3. Results from binomial generalized linear mixed models testing synchrony between regime shifts (significant changes in detrended correspondence analysis axis-1 [DCA1]) and resilience metrics at multiple hierarchical scales. DCA1 and resilience metrics were calculated from avian community data

recorded at North American Breeding Bird Survey routes from 1966 - 2014 aggregated by US Environmental Protection Agency ecoregions. Columns indicate ecoregion level, variable name, coefficient estimate, standard error of coefficient estimate, z-value estimate for coefficient, and P-value estimate for coefficient.

Ecoregion Level	Variable	Estimate	SE	z-value	P-value
LII	Intercept	2.2	0.8	2.8	0.0052
LII	Number of Aggregations	0.045	0.42	0.11	0.91
LII	Cross-scale Redundancy	0.67	0.38	1.8	0.075
LII	Cross-scale Diversity	1	0.37	2.8	0.0048
LII	Within-scale Redundancy	0.3	0.35	0.84	0.4
LIII	Intercept	1.6	0.26	6.1	1.20E-09
LIII	Number of Aggregations	0.21	0.14	1.5	0.14
LIII	Cross-scale Redundancy	-0.3	0.13	-2.3	0.023
LIII	Cross-scale Diversity	0.14	0.13	1	0.3
LIII	Within-scale Redundancy	0.62	0.14	4.6	5.00E-06
LIV	Intercept	0.66	0.15	4.4	1.10E-05
LIV	Number of Aggregations	0.11	0.061	1.8	0.08
LIV	Cross-scale Redundancy	0.35	0.057	6.2	6.70E-10
LIV	Cross-scale Diversity	0.58	0.051	11	1.10E-29
LIV	Within-scale Redundancy	0.23	0.054	4.3	1.90E-05

Resilience-Collapse Test 2: Relationship between cross-scale resilience and community similarity

At the broadest and middle scales (levels II, III), neither initial nor mean resilience metric values significantly predicted changes in community similarity over time (Table 2). But at the finest scale (level IV), initial values of cross-scale diversity (0.0002 ± 0.0001) and number of aggregations (0.0002 ± 0.0001) significantly, albeit weakly, predicted reduced community change (i.e., pushed Jaccard slopes closer to zero—no net community change; Table 2).

Discussion

Using a half-century of subcontinental community data, we provide quantitative support for core predictions of ecological resilience theory regarding how ecological resilience relates to ecological stability and collapse. Per Holling's call in his seminal manuscript on resilience theory (C. S. Holling, 1973), we found resilience is related to but distinct from stability. Importantly,

our results distinguish ecological resilience from concepts allied with stability such as engineering resilience, “bounce-back” time to equilibrium, resistance, and elasticity (L. H. Gunderson, 2000; Pimm, 1984; Standish et al., 2014). We also show that shifts in cross-scale resilience metrics clearly predict and coincide with abrupt community shifts, but at the same time, resilience is weakly related to community change in terms of maintenance of a particular species assemblages over time. We also provide interpretability for cross-scale resilience metrics: we distinguish the roles of functional redundancy and diversity metrics of community collapse and community similarity, respectively (G. Peterson et al., 1998; Walker, Kinzig, & Langridge, 1999), and we show number of aggregations (i.e., scale domains) may be an unresponsive metric if systems reorganize around similar numbers of scale domains during and post-collapse, meaning this metric may only detect extreme collapse events (Angeler et al., 2019b; Roberts et al., 2019).

Our results reaffirm the importance of avoiding the conflation of ecological resilience and ecological stability. Stability theory predicts a particular community composition (e.g., higher species richness) will reduce variance in system functionality but makes no assertions concerning alternative states (Allan et al., 2011; Cardinale et al., 2013; Tilman, 1996; Wagg et al., 2018). Additionally, stability typically does not consider ecological complexity features, such as spatial and temporal scaling structures or thresholds (Baho et al., 2017; Hillebrand et al., 2018). In contrast, resilience theory predicts resilient systems may exhibit wide ranges of variance, community composition will be dynamic and adaptive, and scaling patterns of functional redundancy and diversity within communities (instead of particular community compositions) will determine the ability of a system to remain within one of multiple alternative regimes (Allen, Angeler, Garmestani, Gunderson, & Holling, 2014; Angeler et al., 2019a; Chillo, Anand, & Ojeda, 2011; S. M. Sundstrom et al., 2018). Our results support these differences between stability and resilience: resilience metrics had low degrees of correlation with species richness, a metric that is closely correlated to stability and the ability of a system to “bounce back” from disturbances (Hautier et al., 2015; Ives & Carpenter, 2007; McCann, 2000; Mougi & Kondoh, 2012; Tilman & Downing, 1994). That is, greater richness did not necessarily beget greater resilience. This finding contrasts with a pervasive conflation of richness and resilience (Bellwood & Hughes, 2001; J. Fischer et al., 2007; Oliver et al., 2015; Standish et al., 2014). As expected, cross-scale diversity exhibited the highest correlation with richness, although its correlation was much less than typical cutoffs for collinearity. Cross-scale resilience metrics also did not predict variability in community composition (standard deviation in species turnover) except weakly at the finest scale. This supports the resilience theory prediction that systems may have low stability (high variance in species turnover) but high resilience (Holling, 1973). Our results also support the contention that the concept of ecological stability is nested within ecological resilience: resilience metrics constrained the magnitude of temporal community fluctuations (mean species turnover) but only weakly predicted variability in community fluctuations—which is the purview of stability theory (Angeler and Allen, 2016; Hautier et al., 2015; Mougi & Kondoh, 2012).

Similarly, resilience theory predicts systems with higher resilience will be more likely to retain similar structures and functions over time, but unlike stability, resilience theory makes few predictions on the maintenance of a particular species assemblage (Allen & Holling, 2010;

Bellwood & Hughes, 2001; L. H. Gunderson, 2000). Our results support this premise. Cross-scale resilience metrics were not strongly associated with maintenance of a particular group of species. Instead, resilience metrics predicted maintenance of overall community structure per their synchrony with abrupt community shifts across scales. That is, resilience metrics predict significant abrupt community shifts but not community similarity over time (Angeler et al., 2019b). However, higher resilience metrics did weakly predict maintenance of community composition over time as well as constraining mean species turnover which still supports a connection between species composition and resilience.

The cross-scale resilience model differentiates the roles of functional redundancy and functional diversity, and we corroborate this (Bellwood & Hughes, 2001; Elmqvist et al., 2003; Nash et al., 2016; G. Peterson et al., 1998). For instance, the model predicts losses in critical functions across scaling domains will increase the propensity for ecological regime shifts; but more specifically, redundancy is expected to confer resilience via response diversity (Elmqvist et al., 2003; Walker et al., 1999), while diversity confers resilience via the ability to produce and adapt to novelty (Allen & Holling, 2010; L. H. Gunderson & Holling, 2002). And indeed, we show shifts in functional redundancy across scales (cross-scale redundancy) were asynchronous with community-level change, whereas shifts in functional diversity across scales (cross-scale diversity) were synchronous with abrupt community shifts. Thus, tracking changes in functional redundancy could determine system propensity for regime shifts, and tracking functional diversity could identify periods of reorganization during a disturbance that could result in a regime shift. Importantly, the distinction between functional diversity and redundancy manifested in one of the three scales we analyzed. The reason for this is unclear, but because resilience is a scale-dependent property of ecological systems, the scale-dependent behavior of functional redundancy is not unexpected (Gunderson & Holling, 2002; Allen et al., 2005; Allen et al., 2014). Current research on identifying ecologically meaningful scales (e.g., Angeler, Allen, Uden, & Johnson, 2015) and identifying the spatial boundaries of ecological regimes (i.e., spatial regimes; Allen et al., 2016) stand to clarify the scale-specific behaviors of functional redundancy in reflecting resilience.

Because resilience is an emergent property of complex systems, no single metric can encapsulate it (Angeler & Allen, 2016). The peril of developing resilience metrics is reliance on one or a few to measure a given property of interest. For example, within the stability literature, the diversity-stability debate has long been buffeted by waves of interest in one metric (e.g., species richness) or another (functional diversity, phylogenetic diversity, evenness, etc.) as well as conflicting results from the same metric (Hillebrand et al., 2018; Ives & Carpenter, 2007; McCann, 2000). Likewise, within resilience literature, this has played out in the search for univariate generic early warning signals of regime shifts (Burthe et al., 2016; Clements, Drake, Griffiths, & Ozgul, 2015; Van Nes & Scheffer, 2007) and specific distance-to-thresholds for a specified context (i.e. the resilience of what to what) (Carpenter, Walker, Anderies, & Abel, 2001; Groffman et al., 2006). In contrast, the cross-scale resilience model and its metrics require and assume simultaneous consideration of multiple metrics to quantify resilience (Allen et al., 2005; Angeler & Allen, 2016; S. M. Sundstrom & Allen, 2014; S. M. Sundstrom et al., 2018). We show that individual resilience metrics varied in their relationships with stability and abrupt

community shift metrics, meaning each metric reflects unique aspects of system resilience. Thus, our results support considering metrics of resilience from a multivariate perspective.

For resilience theory to progress, it must have measurable and interpretable characteristics (Carpenter et al., 2005; Cumming et al., 2005; Baho et al., 2017). Although we demonstrate the ability of resilience metrics to compare changes in a system's resilience over time, how to compare relative resilience between systems remains unclear. It is not obvious that a system with more body mass aggregations is more resilient than a system with fewer (Allen et al., 2005). Likewise, it is not clear that when resilience erodes and regime shifts occur that the number of body mass aggregations will change; they may simply reorganize around a similar number of scale domains (Angeler et al., 2019; Gunderson, Allen, & Holling, 2012). Also, it is unclear what increases versus decreases in resilience metrics mean for propensity toward regime shifts (Allen et al., 2005; Fischer et al., 2007). This may be a result of the present "relative" nature of resilience metric units. However, the clarity of signal in resilience metrics that we demonstrate (with noisy data spanning half a century and much of a continent) suggest comparable patterns exist, and comparisons can improve if measurements over time provide refined pictures of system resilience (Angeler & Allen, 2016; Baho et al., 2017). This bodes well for the usefulness of resilience metrics in the Anthropocene, where the need for understanding system resilience to change and collapse is only increasing.

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Task 2. Detect broad-scale shifts in regimes across space and time

Leading indicators of regime shifts using univariate data have been investigated using both simulated datasets and case-studies (e.g. Burthe et al., 2016). Commonly-used early warning indicators for time-series data include an index of variance, the third and fourth moments (skewness and kurtosis, respectively), and critical slowing down (Brock and Carpenter 2006). Although univariate indicators may provide insight into relatively simple systems, like small lakes and isolated wetlands, their reliability as indicators for complex systems is less certain. Carpenter and Brock (2006) use simulations and time series modelling to demonstrate the utility of variance as an indicator of regime shifts within univariate data. Leading indicators can be a reliable warning of impending shift, however, may prove most useful in systems of which we have mapped many of the drivers and processes (Scheffer et al. 2009). Similar studies have transferred these methods to spatial systems, (Kefi et al. 2014). Carpenter et al. (2011) tested the efficacy of early-warning indicators in a whole system, however, reliably measuring the entire complex ecological system is often realistically impossible.

Fisher Information is a metric within the information theoretical framework that estimates the amount of information observed variables carry about an unknown parameter. Contrary to univariate indicators, Fisher Information can be calculated on multivariate datasets, giving it the potential to better capture ecological complexity than univariate approaches (Eason et al., 2016). Rapid change in the amount of information the Fisher Information can be interpreted as change in system configuration, or a regime shift. Specifically, Fisher Information is proposed as an indicator of system orderliness, where periods of relatively high values of Fisher Information indicate the system is in an “orderly” state, possibly fluctuating around a single attractor. A rapid change in Fisher Information should indicate the system is losing order and may be undergoing a reorganization phase. This method is only recently applied to complex social ecological systems and ecosystems (Frieden 1998; Fath et al. 2004).

Despite its established use in identifying the degree of predictability of closed systems in physics, Fisher Information’s utility to rigorously and universally assess complex ecological systems is hitherto unknown. Here, we compare the usefulness of univariate metrics versus Fisher Information as leading indicators of regime shifts in space and time. These metrics were calculated using MatLab v. R2016a.

Materials and Methods

For all Fisher Information analyses, we use avian community abundance data from the North American Breeding Bird Survey (BBS). Spatial analysis consisted of either base-level analysis, where sites were locations within a single military base, or continental-level analysis, where sites were BBS route locations across broad spatial extents (e.g., Florida to New Mexico). Temporal analysis consisted of data collected annually at single sites (i.e., temporal resolution = 1 year). Spatial and temporal Fisher Information calculation does not vary, but interpretation of either differ in that a spatial analysis will identify a spatial regime boundary (Sundstrom et al. 2017) in space within a single year while a temporal analysis identifies the point(s) in time at which a system experiences a regime shift. We identify regime shifts following the methods of

Sundstrom et al. (2017) by visualizing the Fisher Information metric calculated across time and space to declare a regime shift or regime boundary as a site or sites (in space or time) that experiences a significant increase or decrease in Fisher Information and has non-zero first derivative (i.e., $dFI/dt \neq 0$).

Interpreting Fisher Information as an indicator of ecological regime shifts

Here, we define a potential regime change as a point(s) for which the Fisher Information values have a non-zero derivative and at which relatively large changes (manifested as either a sharp increase or decrease) in Fisher Information occurs. Spatial and temporal Fisher Information calculation does not vary, but interpretation of either differ in that a spatial analysis will identify a spatial regime boundary (Sundstrom et al., 2017) within a single time period, whereas temporal analysis identifies the point in time at which the system undergoes a regime shift. We follow published recommendations for interpreting the Fisher Information results in the context of identifying regime shifts (e.g., Karunanithi et al., 2008).

Calculating Fisher Information across spatial transects

To spatially sample BBS routes, we constructed three east-west transects of equally-spaced cells (i.e., grid cells) across the continental United States and parts of Canada. BBS routes are not regularly spaced, and pairwise correlations of adjacent transects is not possible without either (1) binning the Fisher Information calculations using a moving-window analysis, or (2) interpolating the results to regularly-spaced positions in space. To avoid potential biases associated with the former option (i.e. choosing window size, location of data aggregation), we linearly interpolated the calculated Fisher Information within each spatial transect to 50, evenly-spaced points along the longitudinal dimension. The 50 longitudinal points to which we interpolated were the same across each spatial transect, while latitude varied across transects. We used the function `stats::approx()` (with argument `rule=1`) to linearly approximate the Fisher Information. We did not interpolate values beyond the longitudinal range of the original data (i.e., no extrapolation).

Spatial correlation of Fisher Information

If Fisher Information captures and reduces information regarding abrupt changes in community structure across the landscape, then it follows that the values of Fisher Information should be spatially auto correlated. That is, the correlation of Fisher Information values should increase as the distance between points, both within and among transects, decreases. Further, direct comparison of Fisher Information across routes is not possible since Fisher Information is a relative value with no upper limit (i.e. can take on any value between 0 and ∞). In other words, Fisher Information values calculated are not relatively comparable outside of a single spatial transect (Figure 13). Fisher Information is, however, directly comparable within each spatial transect. For these reasons, we can identify spatial regime shifts both within and among spatial transects by using pairwise correlations among two transects to determine whether values of

Fisher Information are consistent across space. We calculated the pairwise correlation (Pearson's) among each pair of adjacent spatial transects (e.g., Figure 13), removing a pair of North-South adjacent points if at least one point was missing an estimate for Fisher Information. Missing estimates of Fisher Information occurs when the original longitudinal range of one transect exceeds the range of the adjacent pair.



Figure 13. Transect sampling design of three, East-West-running transects (colors) used to interpret results of Fisher Information calculation across space. Dots represent BBS route locations.

Results and Discussion

Spatial regimes using Fisher Information

We identified potential regime boundaries within select areas of the continental United States using Fisher Information using multiple methods of data aggregation (or lack thereof) and visualization. Comparing trends in Fisher Information across broad spatial extents among years allows for (1) the identification of areas undergoing a change in ecosystem order, (2) estimation of the relative vulnerability (via Euclidean proximity) of military bases to changes in ecosystem order and (3) the changes in ecosystem order and base vulnerability over time (Figure 14). As expected, investigation of univariate metrics (skewness and kurtosis, respectively) of species abundances ($N = 154$) and the variance index (the eigenvalue of the covariance matrix of the community abundance matrix) using the moving window analysis yield indiscernible results (Figure 15). As such, we omit additional presentation of these metrics in this report.

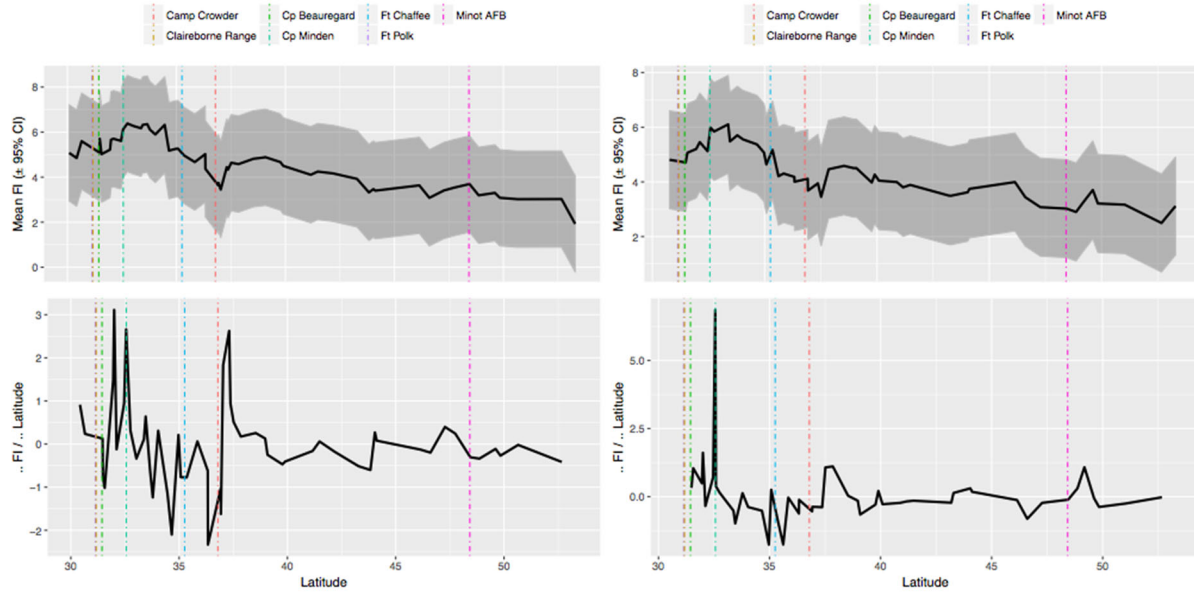


Figure 14. Fisher Information ($\pm 95\%$ confidence intervals), rate of change of Fisher Information over space (dFI/dLatitude), and approximate locations of military bases within the transect in years 2010 (left) and 2014 (right).

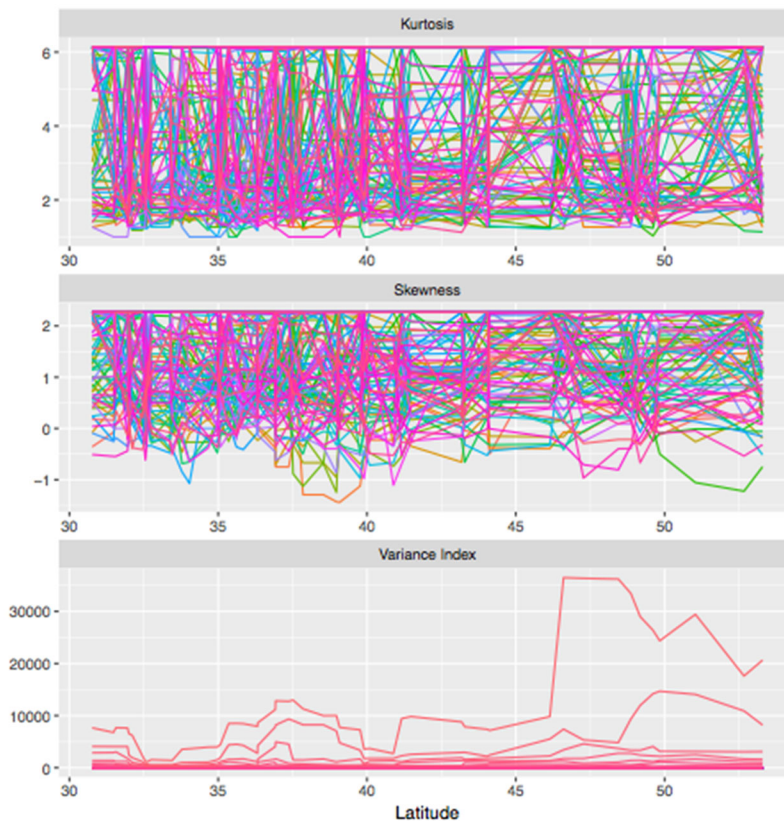


Figure 15. The third and fourth moments (skewness and kurtosis, respectively) of species abundances and the variance index (eigenvalue of the covariance matrix of the abundance matrix) of the North-South route presented in Figure JR1 in year 2010.

Temporal regime shifts using Fisher Information

We ran Fisher Information on Breeding Bird Survey routes across time in and around Eglin Air Force base to determine whether these changes in ecosystem order were echoed at the route-level (16). Fisher information allowed us to compare and contrast the trends in Fisher Information among bird communities within and near Eglin Air Force base (Figure 16). Applying a loess smooth to the Fisher Information trends provides a more pronounced visual interpretation of Fisher Information trend over time (Figure 17).

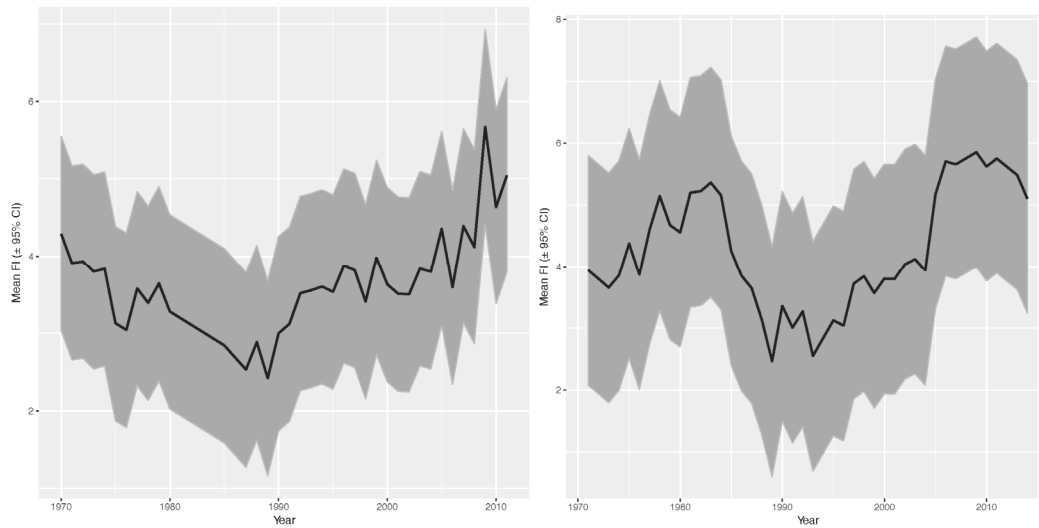


Figure 16. Average Fisher Information across time for Breeding Bird Survey routes within (left) and just west of (right) Eglin Air Force base in Destin, FL, USA.

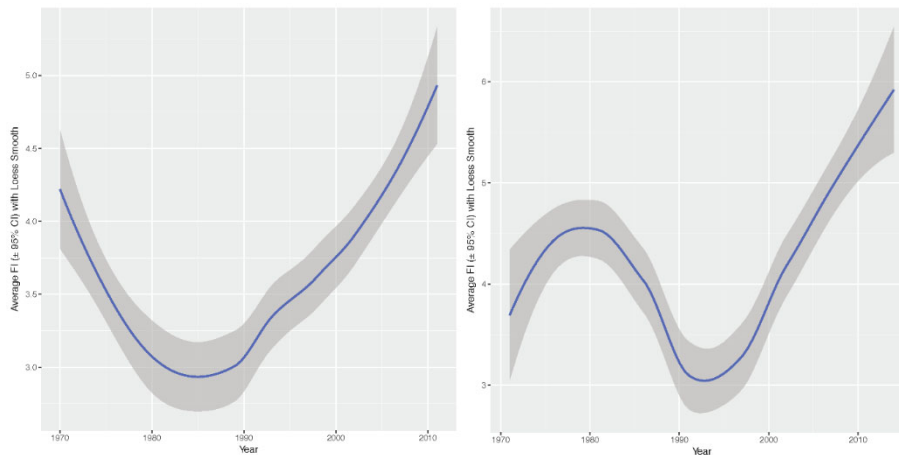


Figure 17. Average Fisher Information with a Loess Smooth across time for Breeding Bird Survey routes within (left) and just west of (right) Eglin Air Force base in Destin, FL, USA.

Rapid increases or decreases in Fisher Information are posited to indicate a change in system orderliness, potentially suggesting the location of a regime shift (Karunanithi et al., 2008). However, of the three spatial transects analyzed in this task (Figure 13), we did not identify clear patterns within nor among spatial transects with respect to Fisher Information.

Temporal analysis of Fisher Information, however, appeared somewhat more useful for identifying regime shifts.

Interpreting the Fisher Information is currently a qualitative effort. Effective regime detection measures should provide sufficient evidence of the drivers and/or pressures associated with the identified regime shifts. Our findings suggest that Fisher Information is useful for temporal regime shift detection for socioecological data (Eason et al., 2016), but care must be taken when interpreting Fisher Information in spatial contexts and for predictive or management planning purposes. However, Fisher Information is clearly more useful and interpretable—even if only evaluated qualitatively—compared to univariate early warning/regime shift detection methods.

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Task 3. Identifying directional changes in spatial regimes using discontinuity analysis of body mass aggregations

Ecological systems are complex and hierarchically organized in space and time (Allen et al., 2014), yet early efforts to quantify ecological resilience and predict regime shifts have focused on the temporal dimension (Dakos et al., 2015; Burthe et al., 2016). This approach has worked 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 prior to regime shifts (Dakos et al., 2012; Carpenter et al., 2011). Advancements have been made by extending early warning indicators such as autocorrelation into spatial contexts (Kefi et al., 2014; Cline et al., 2014; Butitta et al., 2017). However, the theory and methods still assume fixed spatial boundaries of regimes despite being situated in open, complex, and dynamic systems (Clements and Ozgul 2018).

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 (Sundstrom et al., 2017; Roberts et al., 2018). 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 (Sundstrom et al., 2017; Allen et al., 2016). Theory recognizes that all ecological regimes have geographic limits (i.e., spatial boundaries), but those limits may not be fixed or known (Allen et al., 2016). This perspective differs from classical investigations of resilience and regime shifts, which has focused primarily on systems with well-known boundary limits and where critical transitions have been observed over time (Dakos et al., 2015; Scheffer et al., 2001). Many systems have porous boundaries (e.g., grasslands, oceans), many taxa are highly mobile (e.g., birds, pelagic fish), and system boundaries can shift rhythmically or in response to change drivers (e.g., climatic, anthropogenic; Strayer et al., 2003). Thus, there is no single appropriate scale to define spatial regimes in space or how spatial regime boundaries move over time, so this body of theory has only recently advanced as more powerful metrics have emerged in recent years (Clements and Ozgul 2018; Allen et al., 2016).

Here, we build on decades of ecological research on body mass size distributions (Angeler et al., 2016; Spanbauer et al., 2016) to disentangle alternative scientific predictions regarding the behavior of large-scale spatial regimes in an era of global environmental change. One prediction, based on an extension of resilience theory, is that external environmental forcing will cause idiosyncratic behavior in spatial regimes undergoing collapse, similar to the responses of individual species prior to extinction (Drake and Griffen 2010; Doncaster et al., 2016). An alternative hypothesis is that spatial regimes are non-stationary and will be conserved because of strong positive feedbacks, meaning that spatial regime boundaries will move in a directional, orderly trajectory (Sundstrom et al., 2017; Roberts et al., 2018). Disentangling the predictable and orderly from the unpredictable and idiosyncratic provides the foundation for advancing the history of science in early warnings of critical transitions in nature (Clements and Ozgul 2018).

Materials and Methods

Experimental Design

BBS data manipulation

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 (Sauer et al., 2017). 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. 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.

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 (Holling 1992; Sauer et al., 2017). 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 within the Great Plains. For instance, climate change is shifting native and agricultural plant phenologies (Richardson et al., 2013) and geographic centers of plant species distributions (Hovick et al., 2016), woody plant encroachment is causing regime shifts from historically grassland regimes to woodland or shrubland regimes (Engle et al., 2008; Twidwell et al., 2013), fire frequency and size has increased by >400% in the Great Plains (Donovan et al., 2017), energy development such as oil and gas extraction reduced net primary productivity by approximately 4.5 Tg between 2000-2015 (Allred et al., 2015), 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 century (Dunning 2002), and urbanization and population growth in the Great Plains has continually increased in and around already populated areas (Brown et al., 2005). 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 degrees latitude (approximately 2300 km) and east-west from 93 - 97 degrees longitude (approximately 350 km).

Statistical Analysis

Identifying discontinuities

For each route falling within 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 (Dunning 2002). We then used the “discontinuity detector” method (Barichievy et al., 2018) on the log-ranked body masses, which is based on the Gap Rarity Index for detecting discontinuities in continuous data (Stow et al., 2007). 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 (Nash et al., 2014; Sundstrom et al., 2014). Because the discontinuity detector method is known to overestimate discontinuities in observations with low species richness, we removed any routes with < 40 species observed within a given year. We used a power table (Lipsey 1990) to account for sample size (the number of species observed at each BBS route in a given year) and average variance in body masses (Dunning 2002) to adjust the critical d-value (the value based on Monte Carlo simulations that identifies significant discontinuities) where N varied (Allen et al., 1999).

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 route (Spanbauer et al., 2016). 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 within a given year and every column an aggregation size, gap size, or aggregation location (Wickham 2007; Dowle and Srinivasan 2018; R Development Core Team). 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) BBS route and proceeding by order of latitude to the northernmost BBS route (highest latitude). Constrained hierarchical clustering directionally separates multivariate data series into homogeneous, non-overlapping segments; that is, it constrains clusters so that only adjacent, contiguous samples (i.e., a contiguous segment of BBS routes along a spatial transect) are allowed to cluster (Spanbauer et al., 2016; Galzin and Legendre 1987). This method is commonly used to delineate temporally-ordered regimes in paleo community data (Vermaire et al., 2013; Leys et al., 2014) and to detect significant community transitions along spatial transects^{57,58}. To perform constrained hierarchical clustering, we used the “chclust” function with the “CONISS” method from the “rioja” package in R (Juggins 2017).

We used the broken stick model (“bstick.chclust” from the “rioja” package in R) to determine the number of significant clusters (Spanbauer et al., 2016; Juggins 2017; Bennett

1996). 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 (Spanbauer et al., 2016; Leys et al., 2014; Bennett 1996). Because constrained hierarchical clustering identifies homogeneous, non-overlapping areas of self-similarity, significant clusters can be interpreted as regimes, and 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 year (Spanbauer et al., 2016).

Tracking movement in spatial regimes

We tested for non-random movement in spatial regime boundaries over time by fitting generalized additive models (GAMs; “mgcv” package in R) to the northernmost and southernmost spatial regime boundaries (Wood 2011). Because GAMs did not detect nonlinearity in either the northernmost (edf = 1.00, F = 6.56, P = 0.02) and southernmost (edf = 1.00, F = 3.21, P = 0.08) spatial regime boundaries, we estimated the mean rate of movement in spatial regime boundaries via linear regression (Figure 1). We classified the northernmost boundary each year as the spatial regime boundary with the greatest latitude, and 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, 2001). For years in which only one spatial regime boundary was detected (i.e., 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 - 2015 between 37 - 42 degrees latitude to assess the utility of spatial regime tracking for early warnings for land management and the length of planning horizons spatial regimes provided (Figure 4). As above, we quantified spatial regime boundary latitudinal movement over time via linear regression.

Results and Discussion

We analyzed 46-years of avian community body mass distribution data from the Great Plains of North America to identify spatial regime boundaries and then identify patterns in latitudinal spatial regime boundary movement over time. Analyses revealed regional, poleward shifts in both the southernmost and northernmost spatial regime boundaries—which supports our alternative hypothesis of conserved, directional, and relatively ordered movement (Figure 18). The northernmost regime boundary has moved at a greater rate, moving > 590 km from 1970 baselines (0.121 ± 0.080 degrees latitude per year [13 km per year] at 90% confidence) compared to approximately 260 km for the southernmost boundary (0.053 ± 0.051 degrees latitude per year [6 km per year] at 90% confidence). These differential rates of spatial regime movement (northern vs. southern boundaries; Figure 18) match expectations associated with arctic amplification and accelerated change in northern versus southern latitudes of temperate North America (Cohen et al., 2014). Consistent with existing theoretical foundations (La Sorte et al., 2016), the regime moving more quickly also carries with it greater interannual volatility in its location (Figure 18).

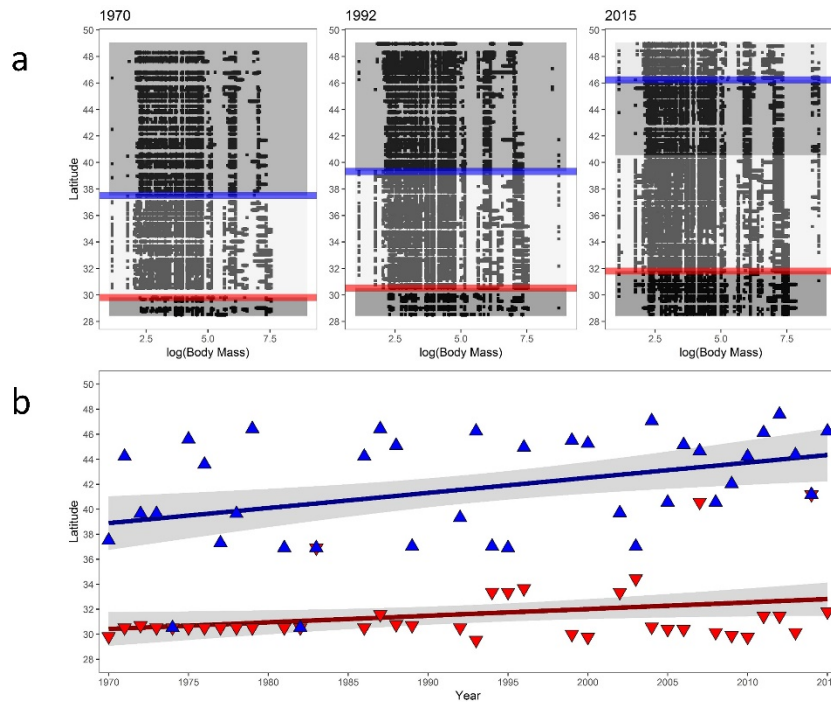


Figure 18. Shifts in spatial regime boundaries demonstrated by breeding bird body mass discontinuities from 1970-2015 in North American Great Plains. a – b, (a) Latitudinal spatial regime boundaries (y-axis) determined by log-ranked avian body mass discontinuities (x-axis). Black dots represent body mass aggregations identified via discontinuity analysis in each breeding bird survey route within the transect. Gray-scale boxes represent spatial regimes, and 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, and lines represent modeled northernmost and southernmost spatial regime boundary movement over time with 90% confidence (grey ribbon). When northernmost and southernmost boundaries were the same (i.e., when only one spatial regime boundary was detected in a year), blue and red triangles overlap.

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% confidence; Figure 19). The number of spatial regimes detected ranged from 0 - 5, with transitory regimes occurring periodically and a fourth, novel spatial regime emerging more consistently in the 2010's decade (i.e., 2010 - 2015; Figure 19). In the early decades of our study, spatial regime boundaries showed some congruence with the Great Plains biome's historic extent (Figure 19). But in subsequent decades, spatial regimes expanded (southernmost regime), moved northward (middle regime), and contracted (northern regimes), providing strong evidence that spatial regimes are rapidly reorganizing and diverging from historic biome extents by the 2010's (Figure 19).

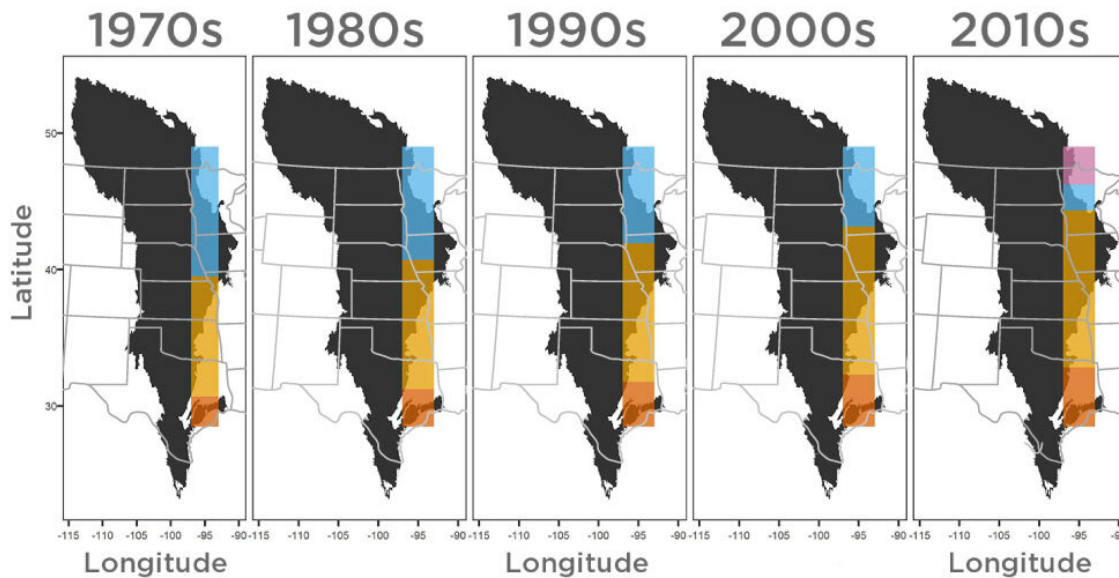


Figure 19. Visualization and tracking of predicted decadal spatial regimes and their boundaries in the North American Great Plains. Black polygons represent the historic Great Plains biome extent. Colored bars represent the predicted extents of spatial regimes within the study area over five decades, and the number of colors represent the average number of spatial regimes detected in each decade.

The cause of northern movement is unknown but 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 several decades, particularly within the Great Plains (Brown et al., 2005; Chen et al., 2011; Johnston 2014; Allred et al., 2015; Donovan et al., 2017; Engle et al., 2008; Boettiger et al., 2013). Irrespective of mechanism, this finding suggests that spatial regimes, and the animal body mass distributions we use to identify regimes, are indeed 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 within the interior of central North America as an illustration (Figure 20). For a network of protected lands in this region, advanced detection would come from tracking spatial regime boundaries within a surrounding window (Figure 20). Knowing the “baseline” boundary in 1970 and its average northward movement pattern, protected lands in the Flint Hills ecoregion had decades of early warning that the entire ecoregion would soon experience an imminent transition, and protected lands in the Western Corn Belt Plains ecoregion had > 40 years of advanced warning (Figure 20). 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 (Boettiger et al., 2013; Hastings and Wysham 2010; Clements et al., 2015). Traditional early warning signals such as critical slowing down, rising variance, and flickering rely on ecological data departing and returning to a baseline, which essentially requires a temporal lag before detecting even a single iteration of a signal (Kefi et al., 2014; Hastings and Wysham 2010; Clements et al., 2015; Scheffer et al., 2009).

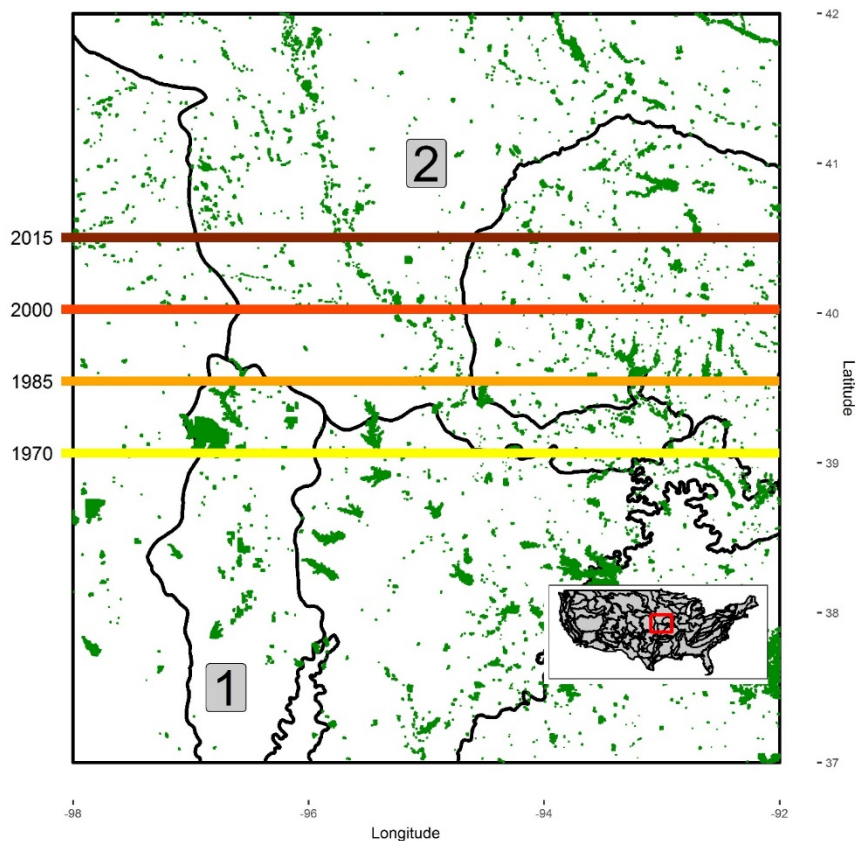


Figure 20. Spatial regime boundary movement between 37 – 42 degrees latitude across a network of protected areas covering in central North America. Black lines indicate level III US Environmental Protection Agency ecoregion boundaries, and green polygons indicate protected areas. The ecoregion labeled No. 1 is the Flint Hills ecoregion, and the ecoregion labeled No. 2 is the Western Corn Belt Plains ecoregion. Predicted spatial regime boundaries (colored horizontal lines) correspond with linear prediction for the years 1970, 1985, 2000, and 2015 ($\beta = 0.032 \pm 0.026$ degrees latitude per year; 90% confidence; $F = 4.093$; $P = 0.052$).

Our analysis suggests that it is now possible for the science of early warning to foster earlier adaptation in environmental management at sub-continental scales, forcing increased awareness of the challenges inherent in the management of stationary ecological conditions at a given location (Biggs et al., 2009). As a moving ecological regime approaches or passes a given location, it becomes increasingly likely that the existing ecological regime will collapse and locations managed to reflect earlier regimes will become a “ghost of regimes past”. Policies that mandate management for ghosts of regimes past, regardless of the current surrounding regime, may be setting themselves up for failure in an era of global change and uncertainty (Craig 2010; Twidwell et al., 2013). Acknowledging this reality has been difficult for ecosystem managers at a given location to accept, and 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, in our example of spatial regime boundaries shifting northward past a conservation land in central North America (Figure 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 (e.g., propagule pressure, avian seed dispersal; Engle et al., 2008; Twidwell et al., 2013). Once these coercive management efforts wane, positive feedbacks will quickly shift to the current basin of attraction of the surrounding spatial regime (Allen et al., 2016; Baho et al., 2014). 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, such as immobile environmental filters (e.g., sandy soil substrates, alkaline soils) or anthropogenic or geographic barriers, exist. In these cases, theory predicts spatial regimes will contract and not “move through” these barriers (Ficetola et al., 2017; Glor and Warren 2011). Over time, if global drivers outweigh local drivers, spatial regime boundaries may exhibit high variance as the local system collapses and reorganizes in the same location. For example, in our study, the southernmost spatial regime boundary (Figure 2) corresponds broadly with the coastal prairie, which is associated with unique sandy soil types and has experienced major landscape fragmentation and conversion via urbanization and energy development (Brown et al., 2005; Chen et al., 2011; Johnston 2014; Allred et al., 2015; Donovan et al., 2017; Engle et al., 2008; Boettiger et al., 2013; Figure 3). Indeed, the southernmost spatial regime boundary exhibited fidelity to the geographic boundary of the coastal prairie from 1970 - 1993 (Figure 1). But in the mid-1990’s, the southernmost boundary began to vary more widely in latitude between its original location to nearly the latitude of the historic northernmost boundary (Figures 1, 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 within conservation ecology have struggled to fully move away from the legacy of equilibrium management, despite numerous resilience-based management frameworks (Twidwell et al., 2013; Briske et al., 2008; Jantz et al., 2015). 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 (Sundstrom et al., 2017; Allen et al., 2016; Birge et al., 2018). 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.

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Task 4. Identify species with stochastic abundance patterns over time

With ongoing environmental change in the Anthropocene, ecosystems are changing at local, regional and global scales (Vellend et al. 2017). For example, multiple global change drivers (e.g. climate, species invasions, agriculture) within the Great Plains of North America affect ecosystems in a south-to-north pattern. In the Great Plains, climatic change is shifting geographic centers of species distributions (Hovick 2016) and native and agricultural plant phenologies (Richardson et al. 2013). Furthermore, woody plant encroachment causes regime changes from historical grassland regimes to shrubland or woodland regimes (Engle et al. 2008). Entire ecoregions in the southern Great Plains have changed to woodlands in the last century, and many ecoregions in the Great Plains are increasingly at risk of fundamental ecological change and regime shifts in the future (Twidwell et al. 2013, Roberts et al. 2019).

Ecologists have had a long-lasting interest in the relationship between disturbances and the responses of ecological communities (Pickett and White 1985, Reynolds 1993, Brawn et al. 2001). Efforts over the last decades have focused on how the structure and function of entire assemblages confer stability to disturbances (Donohue et al. 2013). This research is more recently extended to explore community-disturbance relationships from a resilience perspective. Specifically, the cross-scale resilience model (Peterson et al. 1998; Sundstrom et al. 2018) is used to assess the influence of species structural and functional diversity on resilience for ecosystem (Allen et al. 2005, Angeler et al. 2015a) and landscapes (Angeler et al. 2015b, Roberts et al. 2019).. A major tenet of the cross-scale resilience model is that it accounts for the hierarchical organization of ecosystems and therefore allows assessing disturbance effects on resilience within and across scales of time and space in the system. Accounting for scale in the analysis of disturbance effects is of particular interest because disturbances manifest distinctly at different scales in the system (Nash et al. 2014). For instance, a hail shower may have significantly stronger impact on seedlings compared to trees in a forest (Angeler et al. 2018). Furthermore, disturbances can surpass critical thresholds, which, in addition to scale, is a fundamental component of ecological resilience (Baho et al. 2017), causing the system to shift from one attractor domain to another (i.e. regime shift). It is long recognized that regime shifts produce a fundamental reorganization of ecosystems (Holling 1973), manifested in distinctly different pattern-process relationships and feedbacks between regimes (Allen et al. 2014). These fundamentally altered structures and functions are evident, for instance, in altered abiotic conditions and community structure (Angeler et al 2015c) and the scaling patterns present in the system (Spanbauer et al. 2014).

Much research has so far emphasized the role of dominant species in driving biodiversity and community dynamics in response to environmental change, assuming implicitly that they are key players in ecological dynamics while deemphasizing rare species. In fact, some modeling approaches routinely used by ecologists often exclude rare species to not distort ordinations (e.g., correspondence analysis) or disregard species that are not significantly related to model outcomes (e.g. correlated with canonical axes in redundancy analysis) (but see Baker and King 2010). However, there is mounting evidence that rare species can play an important role in maintaining ecological pattern-process relationships and thus adaptive capacity (i.e. the latent potential of an ecosystem to alter resilience in response to change) after disturbances (Angeler et al. 2019). Mouillot et al. (2013) found that rare species in alpine meadows, coral reefs, and tropical forests comprised functional trait combinations that were not represented by abundant species. These authors suggested that if rare species go extinct, negative effects on ecosystem

processes might result from the subsequent loss of adaptive capacity. Such negative effects may occur even if biodiversity associated with abundant species is high (Mouillot et al., 2013). The importance of rare species is also evident in their ability to replace dominant species after perturbation and maintain ecological functions in the system, which in turn contributes to ecological resilience (Walker et al., 1999). For instance, rare shrub species with larger root crowns than dominant species were able to compensate for the loss of dominant shrub species to mechanical disturbance by re-sprouting prolifically, thus maintaining a shrub-dominated system despite disturbance (Wonkka et al., 2016). This example shows that rare species may contribute an important but, to some extent, unpredictable degree of adaptive capacity to ecosystem change.

In this paper we study the relevance of rare species in the context of regime shifts. Because ecological systems undergo profound reorganization with persistent changes in structure, functions and feedbacks (Angeler and Allen 2016), we were especially interested in assessing whether rare species of one regime might become dominant once a system has shifted to a new regime. We also assess if rare species from one regime remain rare after the regime shift. Understanding these patterns may provide better insight into potential ecological legacies (Johnstone et al., 2016) that rare species from an old regime might leave in a new regime—specifically how they affect critical elements of adaptive capacity and resilience in the new regime. To address our research question, we use time series modeling that infers the temporal scaling structure, and thus the hierarchical patterns necessary for assessing cross-scale aspects of resilience, and the dominant taxa that are contributing to these scale-specific dynamics (“deterministic species”) (Angeler et al. 2009). The modeling also allows for the identification of rare species which, because of their stochastic temporal dynamics (“stochastic species”), are unrelated to any scaling pattern identified (Baho et al. 2014). These stochastic species are considered to encompass rare taxa in this study, where rarity is defined as species occurring along a gradient from frequent incidences with low abundances to sporadic occurrences with higher abundances throughout the study period.

We study the relevance of potential ecological legacies of stochastic species using breeding bird communities in the American Great Plains as a model system. Because of the south-to-north movement of ecoregions or spatial regimes (Roberts et al. 2019), we assess how stochastic species of the northern regime may potentially influence stochastic and deterministic patterns once it gets encroached by and shifts to an expanding southern regime. We used a time-for-space substitution, an approach commonly used in ecology (Pickett 1989), especially in a climate change context (Blois et al. 2013). Modern regime shifts often unfold at time scales that are not covered by routine monitoring (Spanbauer et al. 2014). Space-for-time substitutions overcome this common problem in regime shift research by comparing spatially independent units that already occur in alternative regimes. In our specific case, as the southern regime is suggested to eventually expand into the northern regime with ongoing climate change (Roberts et al. 2019), we assess if and how many stochastic species of the “vulnerable” (northern) regime will show either stochastic or deterministic patterns in the “expanding” (southern) regime. We also assess if these species occur at one or different temporal scales of the expanding regime, which allows us to determine their contributions to cross-scale resilience in the expanding regime. This might provide insight into the dynamically changing spatial resilience of landscapes and how this might affect management and conservation efforts for ecosystems and species with ongoing climate change (Allen et al. 2016).

Material and Methods

Data and study setup

We collected 47 years of data ranging 1968 - 2014 from the U.S. Geological Survey Breeding Bird Survey data (BBS) of North America. The data contain avian community composition that is collected by qualified observers along georeferenced, permanent roadside routes across North America (Sauer et al. 2017). These data are publicly available. Along each *ca* 39.5 km route, observers make 50 stops once every 0.8 km where they conduct point-count surveys. During each survey, observers stand at the stop and record for three minutes the abundance of all bird species that are visually or aurally detected within a 0.4 km radius. Surveys start thirty minutes before local sunrise and last until the entire route is finished. To increase uniformity in probability of bird detection, surveys are conducted only on days with little or no rain, high visibility, and low wind.

We removed all aquatic species from the Anseriformes, Gaviiformes, Gruiformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes, and Suliformes families from the analysis because of known negative observation biases for waterfowl compared with terrestrial avian families (Holling 1992). We also removed hybrids and unknowns, and we condensed subspecies to their respective species.

Time series data across routes were heterogeneous with many missing data, but three transects were found suitable for analysis for each of the two regimes studied. The three transects, which together comprised 82% of the total species pool in the southern regime and 86% in the northern regime, were averaged to obtain exhaustive species occurrences and to facilitate the comparison of species distributions between spatial regimes. For this study, we selected a southern (latitudes: 28.9 – 29.7; Western Gulf Coastal Plains) and a northern spatial regime (latitudes: 31.8 – 33.4; South Central Plains) for analyses. These regimes were chosen because of biogeographical shifts (northward movement of southern regimes) with ongoing climate change (Roberts et al. 2019).

Statistical Analysis

Time series models

All statistical analyses were carried out in R 3.0.2 (R Development Core Team, 2012) using the ‘aem.time’ function (AEM package, Blanchet and Legendre (2013), packages nlme (Pinheiro et al., 2008), and the ‘quick PCNM’ function (PCNM package, Legendre et al., 2013). Asymmetric Eigenvector Maps (AEM) were extracted from a set of orthogonal temporal variables that were calculated from the time vector consisting of 47 steps between years 1968 and 2014. These AEMs are used as explanatory variables to model temporal relationships in the BBS data. In the case of AEM, the first variable models linear trends and subsequent variable show sine-wave patterns (Legendre and Legendre, 2012), which allows assessing directional change and different inter-annual and decadal variation in the BBS. These extracted temporal variables are then used as explanatory variables in the time series models using redundancy analysis (RDA) (Angeler et al. 2009). Two time series models were constructed, one for the southern regime and one for the northern regime, which consisted of 122 species and 111 species, respectively, as response variables.

RDA selects significant temporal variables (AEMs) using forward selection. The selected variables are linearly combined in the RDA models to extract temporal structures from the bird species matrices. The modeled temporal patterns that are extracted from the data are collapsed onto significant RDA axes, which are tested through permutation tests. These RDA axes are then used to distinguish deterministic from stochastic species in the analysis. The R software generates linear combination (lc) score plots, which visually present the modeled temporal patterns that are associated with each RDA axis. That is, individual RDA axes indicate fluctuation patterns at different temporal frequencies or scales. All bird species raw-abundances averaged from three transects per regime were Hellinger transformed prior to the analysis (Legendre and Gallagher 2001).

Correlation of Bird Taxa with Modeled Spatial Patterns

Following Angeler et al. (2015), we used Spearman rank correlation analysis to relate the raw abundances of individual bird taxa with the modeled temporal patterns (lc scores) associated with the RDA axes of both models. In this way we identified taxa that contributed significantly to the temporal dynamics revealed by the RDA (that is, deterministic species). Those taxa that were not associated with any significant canonical axis were identified as stochastic species.

Next we examined whether stochastic species from the northern regime occur as either deterministic and/or stochastic patterns of the southern regime. This provides insight regarding how species change may alter the resilience of the northern regime once it is invaded by the southern regime with climate change.

Results and Discussion

Results

The analyses from the time series modeling of BBS data revealed significant temporal structure in both spatial regimes between 1968 and 2014. The overall variance explained by AEM models was high (adjusted R^2 values; northern regime, 0.65; southern regime 0.63). The models revealed fluctuation patterns at distinct temporal scales (Figure 21). AEM revealed temporal dynamics associated with five and six significant RDA axes for the northern and southern spatial regime, respectively. Comparing both regimes, the temporal patterns were similar at RDA 1 and RDA 2. RDA 1 displayed a marked component of monotonic change in community composition. RDA 2 showed hump-bell shaped patterns. The remaining RDA axes indicated higher temporal variability of bird community structure within and between both regimes (Figure 21).

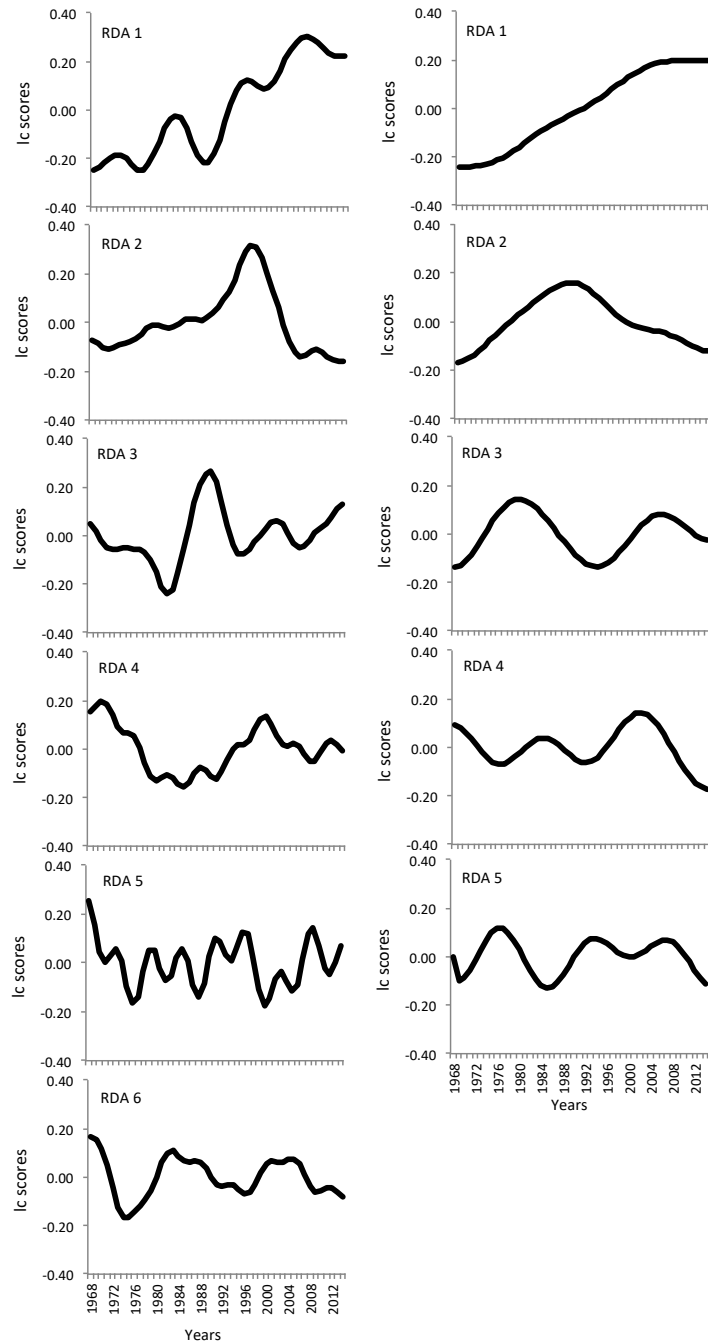


Figure 21. Linear combination (lc) score plots showing significant temporal patterns associated with different RDA axes in the time series models. Panels on the left represent the northern regime that becomes vulnerable to the invasion of the southern regime (right panels) due to climate change.

From the 122 bird species present in the southern regime 87 (71%) were deterministic and 35 (29%) stochastic. From the 110 taxa present in the northern regime 86 species (78%) were deterministic and 24 taxa (22%) stochastic. Across deterministic species, most taxa were correlated with RDA 1 (56 northern regime, 45 southern regime), followed by RDA 2 (19 northern, 12 southern) (Table 4). Only a few, generally fewer than 8 species correlated with the remaining RDA axes, except RDA 4 (19 species) of the southern regime model (Table 4).

Table 4. Number of bird species correlating significantly with significant RDA axes in time series models (i.e. deterministic species) of the northern and southern regimes. Shown are also the number of stochastic species (uncorrelated with any RDA axis), and the total number of species in the data sets.

Regime	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5	RDA 6	Deterministic	Stochastic	Total
Northern	56	19	4	4	3	--	86	24	110
Southern	45	12	8	19	1	7	87	35	122

From the 24 stochastic species present in the northern regime, 10 were also found in the southern regime (Table 5), meaning that less than half of taxa of the former regime occurred in the latter. From these, 5 species (*Thyromanes bewickii*, *Bubo virginianus*, *Pandio haliaetus*, *Tachyneta bicolor*, *Vireo flavifrons*) remained stochastic and 5 species correlated with different RDA axis of the southern regime (Table 5). Specifically, *Dumetella carolinensis* and *Buteo swainsoni* correlated with RDA 1, *Eremophila alpestris* and *Passerina ciris* with RDA 2, and *Setophaga americana* with RDA 3 while no stochastic species of the northern regime were found at RDAs 4, 5 and 6 of the southern regime model. This indicates that stochastic species can become deterministic at different scales in a new regime.

Table 5. Stochastic species from the northern regime and their occurrences as deterministic (correlation with significant RDA axes in parenthesis) or stochastic species in the southern regime. Northern species that were no longer present in the southern regime are also shown.

Northern regime	Southern regime		
Stochastic species	Deterministic species	Stochastic species	Not present
<i>Dumetella carolinensis</i>	X (RDA 1)		
<i>Buteo swainsoni</i>	X (RDA 1)		
<i>Eremophila alpestris</i>	X (RDA 2)		
<i>Passerina ciris</i>	X (RDA 2)		
<i>Setophaga americana</i>	X (RDA 3)		
<i>Thyromanes bewickii</i>		X	
<i>Bubo virginianus</i>		X	
<i>Pandion haliaetus</i>		X	
<i>Tachycineta bicolor</i>		X	
<i>Vireo flavifrons</i>		X	
<i>Spinus tristis</i>			X
<i>Falco sparverius</i>			X
<i>Setophaga ruticilla</i>			X
<i>Strix varia</i>			X
<i>Bombycilla cedrorum</i>			X
<i>Anthus vociferus</i>			X
<i>Leuconotopicus vilosus</i>			X
<i>Parkesia motacilla</i>			X
<i>Seiurus aurocapilla</i>			X
<i>Vireo gilvus</i>			X
<i>Sitta carolinensis</i>			X
<i>Meleagris gallopavo</i>			X
<i>Helmitherus vermivorum</i>			X
<i>Dendroica petechia</i>			X

Discussion

That ecological systems undergo substantial structural and functional change after regime shifts is increasingly supported by empirical evidence (e.g., Spanbauer et al. 2016). The results of this study build on this existing body, adding an ecological legacy component (Johnstone et al. 2016); specifically, how stochastic species from one regime might contribute to the adaptive capacity and resilience of a new regime.

We use time series modeling to quantify resilience in both spatial regimes based on the cross-scale resilience model that helped us distinguish between deterministic and stochastic species in the data set (Baho et al. 2014). Furthermore, the approach allowed us to assess temporal scales present in the regimes and at which scales individual species fluctuate. This distinction is an objective representation of dynamics of abundant and rare species in the community (Baho et al. 2014), which allows for a refined assessment of community change opposed to approaches based on arbitrary delineations of species rarity (Gaston 1994) or whole communities. Results show that deterministic species dominated the temporal dynamics in both spatial regimes, with the contribution of stochastic species being below 29%. While these results deviate from the notion that rare species dominate ecological communities (Magurran 2013), we emphasize that our results are based on modeling which explicitly accounts for species abundance changes and redundancies in these patterns over a defined time period. The approach therefore differs from methods based on snapshot samples that require different methods for assessing rarity.

Results revealed that only 10 out of the 24 stochastic species of the northern regime occurred in the southern regime. This finding is not inconsistent with regime shift theory and further supports that regime shifts cause substantial ecological reorganization (Angeler and Allen 2016). A novel finding of our study is the partitioning of these species between deterministic and stochastic patterns in the new regime. The modeling revealed that 5 stochastic species from the northern regime remained stochastic and the other 5 became deterministic in the southern regime. These 5 species were associated with three different temporal scales in the southern regime model. Because these scales were relatively species rich, our results suggest that these stochastic species contribute a relatively low degree of within-scale and cross-scale resilience and adaptive capacity in the southern regime. It has been suggested that rare species can compensate for the loss of dominant species and maintain the adaptive capacity of ecosystems after disturbances (Walker et al. 1999, Wonkka et al. 2016). Our results show that this does not necessarily need to be the case when systems undergo a regime change. Only 10 stochastic species of the northern regime were represented in the bird community of 122 species of the southern regime, which suggests that stochastic species from the northern regime may only leave a marginal ecological legacy in southern regime.

Our study is based on space-for-time substitutions in which a regime change is only implicit. That is, rather than assessing explicitly regime changes resulting from northward migration of spatial regimes, our approach compared community dynamics between regimes, assuming that over time the southern regime will turn into the northern regime. Given our study design, the potential role of ecological legacies is therefore also only indirectly assessed because we lack the explicit sequential replacement of regimes and their species pools. While space-for-time substitutions have been criticized they are still a valuable alternative to long-term studies (Pickett 1989), particularly in a climate change context (Blois et al. 2013). Space-for-time substitutions are therefore particularly useful for regime shift research which is often limited by

monitoring data that do not cover relevant scales of ecological change, which can be slow, particularly in a spatial context. The need to account for both space and time in the assessment of spatial resilience further underscores the utility of space-for-time substitutions as an important approach in spatial regime shift research (Allen et al. 2016), especially given the fast biogeographical changes on a rapidly changing planet.

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Task 5: Detect early warnings of regime shifts within military installations

Predicting where regime shifts are likely to manifest is one of the grand challenges for ecologists this century (Biggs, Carpenter, & Brock, 2009; Clements & Ozgul, 2018; Scheffer, Carpenter, Foley, Folke, & Walker, 2001). A central premise of ecological theory is that ecological communities will warn of a pending regime shift, but detection has proven elusive in systems with open boundaries and strong spatial order of regime change (Burthe et al., 2016; Hastings & Wysham, 2010). In such systems, multiple alternative regimes can exist alongside each other within a given spatial extent (Hoffmann et al., 2012; Roques, O'connor, & Watkinson, 2001; Scheffer & Carpenter, 2003). For instance, within areas historically dominated by grassland regimes, isolated shrub island regimes and tree-dominated regimes can appear, disappear, expand, or contract according to fire regimes (Ratajczak, Nippert, & Ocheltree, 2014). But because traditional regime shift prediction methods do not explicitly consider spatial order (e.g., boundaries between alternative regimes existing simultaneously on a landscape) and do assume fixed boundaries, these methods require a sufficient proportion of the system to shift to an alternative regime and exhibit a particular temporal pattern before they register a regime shift signal (Kefi et al., 2014; Wang et al., 2012). Not only will this lead to lags in regime prediction, it does not account for spatial order of alternative regimes in open systems (C. R. Allen et al., 2016). Timely prediction of regime shifts in open, complex systems will require concepts and methods that explicitly incorporate spatial dimensions (Clements & Ozgul, 2018; C. P. Roberts et al., 2018).

The concept of spatial regimes has attempted to resolve these issues for open, complex systems (C. R. Allen et al., 2016; C. P. Roberts et al., 2018; Sundstrom et al., 2017). Spatial regime posit alternative regimes can exist within a given spatial extent, alternative regimes manifest strong spatial order including self-similarity near the spatial center of regimes and measurable boundaries (at a given scale), regime boundaries can shift, expand, and contract to displace other regimes, and the vulnerability to regime shifts increases near the boundaries of alternative regimes (C. R. Allen et al., 2016; C. P. Roberts et al., 2018). To date, spatial regimes have been operationalized by identifying sharp, spatially-explicit transitions in biotic communities or structure (Sundstrom et al., 2017). However, current methods for operationalizing the spatial regimes concept have met challenges (Clements & Ozgul, 2018). For example, multivariate clustering methods rely on discrete, non-statistical (i.e., lacking a hypothesis test) boundary cutoffs, meaning uncertainty in regime identification and the gradual or discrete natures of boundaries cannot be easily obtained (C. Roberts, Allen, Angeler, & Twidwell, 2019). Additionally, like related boundary detection and gradient analysis concepts, spatial regimes methods have also largely been restricted to one-dimensional space, for example identification along transects (Fagan, Fortin, & Soykan, 2003; C. Roberts et al., 2019; Sundstrom et al., 2017).

Wombling, a method proposed by and named after Womble (1951), has potential to overcome these issues in operationalizing spatial regimes. Wombling was developed to avoid subjective, discrete classification schemes of ecological systems (Barbujani, Oden, & Sokal, 1989; Diniz-Filho, Soares, & Campos Telles, 2016; Womble, 1951). It is designed to provide probabilistic estimates of the likelihood of boundaries between ecological entities without requiring *a priori* system knowledge (Barbujani et al., 1989), and it incorporates two spatial dimensions, granting it the ability to detect spatial boundaries in open, complex systems such as terrestrial landscapes (Kent, Levanoni, Banker, Pe'er, & Kark, 2013). Wombling can detect

boundaries using univariate or multivariate data. Wombling has been used in landscape genetics studies for identifying landscape barriers of gene flow and spatially-distinct genotypes (Barbujani & Sokal, 1990; Diniz-Filho et al., 2016), mapping disease spread boundaries in order to identify sources of disease (Ma, Carlin, & others, 2007), and providing spatially explicit estimates of vulnerability and barriers to spread of invasive species (Fitzpatrick et al., 2010).

Wombling could potentially be translated into a regime shift prediction method by inputting spatially-explicit biotic community composition data and tracking changes in wombling-identified boundaries across space, over time (Diniz-Filho et al., 2016; C. P. Roberts et al., 2018). For instance, in an open, complex system hosting multiple alternative regimes, wombling could be used to identify and track spatial regime boundaries in situations where 1) one regime expands, displacing its neighboring regime, 2) boundaries between two or more regimes remain stationary over time due to negative feedbacks that maintain regime boundaries, 3) one regime becomes dominant and manifests self-similarity in its wake, or 4) landscapes, and the regimes they contain, are highly fragmented (C. R. Allen et al., 2016; C. P. Roberts et al., 2018). In all of these situations, the predicted vulnerability of a given location to a regime shift (i.e., one spatial regime being displaced by another) would be the spatial distance of a wombling-identified boundary to the given location and the pattern of change in boundary location over time; that is, if the boundary is moving toward the location, it would have greater vulnerability to a regime shift (C. R. Allen et al., 2016; C. P. Roberts et al., 2018; C. Roberts et al., 2019).

Here, we test the ability for wombling to (i) identify boundaries between ecological regimes, and (ii) provide spatially-explicit prediction of the vulnerability of one regime to be displaced by another, corresponding to a change in spatial regime boundaries. To accomplish this, we use 26 years of bird community to test strength and scales at which wombling relates to well-known and previously established boundaries of vegetative regimes. We then employ advances in spatial informatics to visualize and interpret how wombling tracks shifting spatial regime boundaries over time.

Materials and Methods

Study site

We conducted this study at Fort Riley Army Base, Kansas, USA (39.09999 N 96.81666 W). Fort Riley is a US military reservation encompassing approximately 41,170 ha. It is located in the Flint Hills ecoregion of the North American Great Plains. The Flint Hills are characterized by strong topographic relief, with sharp inclines from lowland ravines with gallery forests and shrublands to relatively flat uplands (Omernik & Griffith, 2014).

Fort Riley is an ideal study site at which to test regime shift applications of wombling due to its ecological history and suite of alternative regimes (Briggs, Hoch, & Johnson, 2002). Like the rest of the Flint Hills, Fort Riley can support two major alternative regimes: a grass-dominated regime and a tree-dominated regime (Ratajczak et al., 2014). Historically, tallgrass prairie covered most of the Flint Hills, including big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*) (Briggs, Knapp, & Brock, 2002; Limb, Engle, Alford, & Hellgren, 2010). Woody plants, historically rare and limited to areas where they could escape fire (e.g., ravines, rocky outcroppings), include eastern redcedar (*Juniperus virginiana*), sumac (*Rhus* sp.), and roughleaf dogwood (*Cornus drummondii*) (Briggs et al., 2005). These vegetative regimes also correspond with specific avian

communities—a suite a grassland bird species that respond negatively to tree cover and require large tracts of grassland, and a suite of forest bird species that are tied to tree cover but can occur in fragmented landscapes (Fuhlendorf, Woodward, Leslie, & Shackford, 2002; Grant, Madden, & Berkey, 2004; Thompson, Arnold, & Amundson, 2014).

Due to fire suppression implemented by European colonists, woody plants have expanded out from their former local boundaries and are invading grasslands (Twidwell et al., 2016). However, within Fort Riley, fire disturbances (both random ignitions from military training and planned, prescribed fires) occur much more frequently and during weather conditions of lower humidity and higher wind speed than the surrounding Flint Hills, meaning Fort Riley’s fire regimes are more similar to historic fire regimes that maintained tallgrass prairie regimes (Ratajczak et al., 2016; Ratajczak, Nippert, Briggs, & Blair, 2014). But due to regional pressures and uneven fire regimes across the installation, Fort Riley has also experienced displacement of grassland regimes by tree regimes. Altogether, these competing pressures and regimes make it likely that the situations in which wombling could identify spatial regimes and predict vulnerability will occur at Fort Riley, enabling a test of wombling’s regime shift prediction applications (Diniz-Filho et al., 2016; Womble, 1951).

Data

We tested wombling as a predictor of regime shifts by applied wombling to georeferenced bird community composition data and comparing boundaries identified by wombling to boundaries of the two major alternative regimes that occur at Fort Riley—tree regimes and grass regimes. Thus, we collected 26 years of bird community composition data and vegetation data from across Fort Riley. Because bird communities are known to strongly differ between grassland and tree regimes, wombling should relate to tree-grass boundaries at some set of scales.

Vegetation data

We used a novel raster dataset that provides annual percent cover of plant functional groups at a 30 x 30 m resolution (M. O. Jones et al., 2018). This dataset masks urbanized areas (roads, buildings) and water (lakes, ponds, streams, rivers). We extracted percent perennial herbaceous plant cover and percent tree cover by cell. We used these two functional groups to identify spatial boundaries between the two major alternative regimes occurring at Ft. Riley—a tree-dominated regime and a grass-dominated regime (Briggs et al., 2002; Ratajczak et al., 2016).

Bird community data

Using a stratified random design, 59 bird community sampling locations were established in 1991. Stratified classes originated from soil-land cover type combinations and distributed a number of sampling locations within each class proportional to its land area at Ft. Riley. Sampling locations were surveyed from 1991 - 2017 during the breeding season (May - June). Most locations were surveyed annually, but some gaps in survey years occurred for 3 sampling locations. 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. The same azimuth was used for all years. Surveyors walked the length

of the transect in 6 minutes, stopped for 8 minutes at the end of the transect, and then walked back to the beginning of the transect for 6 minutes. Surveyors recorded the number and species of all birds seen or heard during these surveys.

Boundary identification

Vegetative boundaries: spatial covariance

We quantified spatial boundaries between tree and grass regimes by calculating spatial covariance between percent tree and percent grass cover for each raster cell via moving windows (D. Uden et al., 2019; Wagner, 2003). To test the strength and scales at which wombling related to known regime boundaries, we calculated spatial covariance at moving window sizes of 9 (3 x 3), 64 (8 x 8), 169 (13 x 13), 529 (23 x 23), and 1089 (33 x 33) pixel neighborhoods.

Spatial covariance ranges continuously from positive to negative values. Positive values indicate spatial synchrony in tree/grass cover (i.e., as tree cover increases, grass cover increases), values near zero indicate spatial similarity (i.e., a given raster cell is surrounded by either all trees or all grass), and negative values indicate spatial asynchrony in tree/grass cover (i.e., as woody cover increases, grass cover decreases). Because tree and grass are alternative regimes, spatial covariance values across Ft. Riley mainly ranged from near zero to strongly negative. 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.

Bird community boundaries: wombling

We used wombling to identify boundaries in bird communities. Specifically, we used a geographically weighted regression (GWR) as a generalized wombling method for point-based data. GWR 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 locations of abrupt change; that is, boundaries. We first used a Hellinger transformation to correct for rare species and then performed principal components analysis (PCA) on the full transformed dataset (all years, all sampling locations) (Dray, Legendre, & Peres-Neto, 2006). We used the first axis of the PCA as the 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 the GWR for each year of our data (1991 - 2017). Overdispersion can cause GWR to fail to converge, so we removed any years in which overdispersion occurred.

Testing wombling

Can wombling identify boundaries between ecological regimes?

We quantified the relationship between boundaries detected by wombling (high R^2 values derived from GWR) and known spatial regime boundaries (negative spatial covariance in tree/grass cover) by developing separate a set of candidate generalized additive mixed models

(GAMMs) with different combinations of spatial covariance window sizes (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In each model, we set R^2 as the response variable and spatial covariances (the value of the raster cell nearest each bird sampling location) as the smoothed predictor variable. We allowed intercept to vary by year. We used Akaike Information Criterion corrected for small sample sizes for model selection.

We tested the spatial relationship between wombling boundaries and known spatial regime boundaries by with the same set of candidate GAMMs as above. In this case, we set R^2 as the response variable, but we used distance (m) to nearest spatial regime boundary for each window size as smoothed predictor variables. We considered the nearest spatial regime boundary to be the closest raster cell to each bird sampling location with a scaled spatial covariance value of ≤ -1 . This cutoff ensured near zero covariance values were excluded. Because spatial covariance raster pixel size was 30 x 30 m, distances ≤ 30 m would indicate the nearest boundary was the cell the bird survey location fell within. Thus, we replaced any distance ≤ 30 m with 30 m. We allowed intercept to vary by year.

Can wombling predict changes in spatial regime boundaries?

We used spatial informatics to visually determine if wombling predicted and tracked changes in spatial regime boundaries. We mapped spatial covariance rasters for each year of bird community data that we analyzed (i.e., years that GWR did not fail). We used the spatial covariance window size (scale) that most strongly associated with wombling boundaries. We then mapped locations of bird sampling locations as points on top of spatial covariance rasters by year. We set these points to vary in size according to their wombling R^2 value for each year, with larger R^2 values corresponding to larger point sizes.

Finally, we assessed the ability of wombling to predict changes in spatial regime boundaries at two spatial extents. First, we visually inspected selected portions of the study area that 1) were likely to exhibit shifts in spatial regime boundaries (regime shifts) due to encroaching tree regimes into grassland regimes, 2) were likely to have maintained stable tree-grass spatial regime boundaries due to receiving consistent application of fire and being near the center of a grassland regime, 3) were initially boundaries between tree-grass regimes and became centers of tree regimes as tree regimes displaced grasslands, and 4) were highly fragmented by tree-grass boundaries. Specifically, we chose an area that is less disturbed and is near a ravine from which woody plants could spread, an area that was consistently and heavily disturbed by random and prescribed fires and military training, an area near a major river that would have historically hosted a tree regime and would have provided a source for tree encroachment of grasslands, and an area known to be highly fragmented by tree-grass boundaries. If wombling is able to predict and track changes in spatial regime boundaries, wombling values should increase in areas where spatial regimes boundaries are shifting (e.g., where woody plant regimes encroach on grasslands), remain relatively stable where regime boundaries do not change or near the center of spatial regimes (e.g., in the middle of a grassland, the boundary between upland forests and riparian forests), and decrease as spatial regime boundaries expand away from them (e.g., locations initially at the boundary of tree-grass regimes that become centers of tree regimes due to tree encroachment of grasslands).

Second, we visually inspected wombling patterns at the extent of the entire study area.

Results and Discussion

Wombling identifies boundaries between ecological regimes

Vegetative boundaries and wombling boundaries

Model selection revealed considerable model uncertainty, with the first four models having similar AICc weights ranging from 27% (top model) to 20% (fourth model; Table 6). However, the four top models produced similar patterns across spatial covariance window sizes. We only interpret the top model here.

Table 6. Model selection using AICc for two questions: 1) assessing relationships between vegetation (tree/grass) and bird community boundaries and 2) determining how bird boundaries responded to distance to vegetation boundaries. Columns indicate the question, the model covariates/smooth terms, the total number of covariates, the estimated AICc value, the delta AICc, and model weight.

Question	Model Covariates	K	AICc	Delta AICc	AICc Weight
Relationship	13, 33	7	247.97	0.00	0.27
Relationship	3, 13, 33	9	248.11	0.15	0.25
Relationship	13, 23, 33	9	248.22	0.25	0.24
Relationship	3, 13, 23, 33	11	248.56	0.59	0.20
Relationship	global	13	252.29	4.32	0.03
Relationship	23, 33	7	296.40	48.43	0.00
Relationship	3, 33	7	317.84	69.88	0.00
Relationship	3, 8	7	353.51	105.54	0.00
Distance to Boundary	3, 13, 33	9	243.49	0.00	0.62
Distance to Boundary	3, 13, 23, 33	11	244.97	1.49	0.30
Distance to Boundary	global	13	248.62	5.14	0.05
Distance to Boundary	13, 33	7	249.89	6.40	0.03
Distance to Boundary	13, 23, 33	9	251.97	8.49	0.01
Distance to Boundary	3, 33	7	255.84	12.35	0.00
Distance to Boundary	23, 33	7	281.45	37.97	0.00
Distance to Boundary	3, 8	7	296.80	53.32	0.00

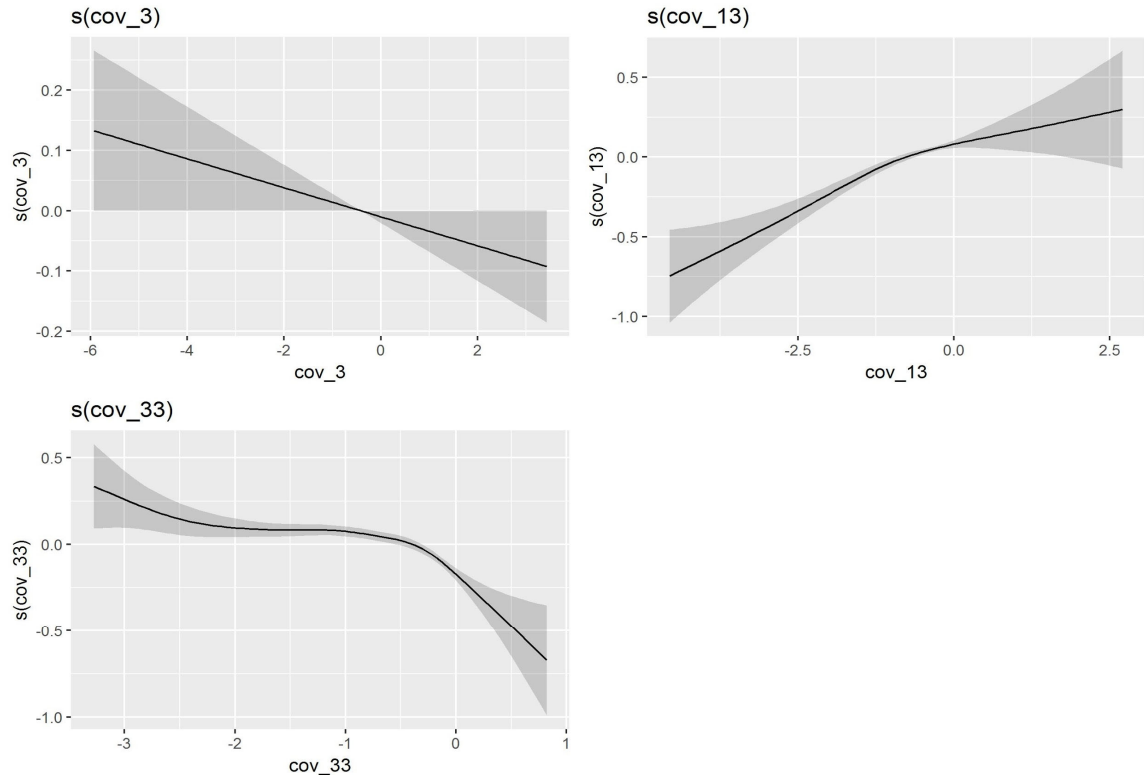


Figure 22. Generalized additive mixed models demonstrate the relationship between spatial regime boundaries derived from a “wombling” method applied to bird community data with known vegetative tree-grassland spatial regime boundaries derived from remotely-sensed spatial covariance. The y-axis depicts the smoothed, predicted relationship between wombling values (R^2) and spatial covariance values (i.e., not the predicted wombling values). The x-axis shows a scaled range of spatial covariance values. Higher wombling values indicate greater likelihood and strength of a boundary. Spatial covariance values at or near zero indicate no tree-grass boundary, and negative spatial covariance values indicate increasingly stark tree-grass regime boundaries.

In the top model, wombling boundaries corresponded to known spatial regime boundaries at window sizes of 90 x 90 m, 390 x 390 m, 690 x 690 m, and 990 x 990 m (Table 6). At the smallest window size (90 x 90 m), wombling values (R^2) had a linearly negative relationship with spatial covariance (Figure 22). However, at the next largest window size (390 x 390 m), wombling values exhibited a nonlinear relationship with spatial covariance, with a relatively flat—but highly uncertain—pattern at positive spatial covariance values; and this transitioned to a positive relationship between wombling values - spatial covariance at negative spatial covariance values (Figure 22). And at the largest window size (990 x 990 m), wombling values were strongly negatively associated with positive spatial covariance, and then the relationship flattened out until another shift to negative association at very low spatial covariance values (Figure 22).

Distance to boundary

The top model relating wombling boundaries to distance to known regime boundaries contained the smallest (90 x 90 m), middle (390 x 390 m), and largest (990 x 990 m) spatial

covariance window sizes (Table 6). Model certainty was greater in this case, with the top model accounting for 62% of AICc weight and second model accounting for 30% of AICc weight (Table 6).

In the top model, at the smallest window size (90 x 90 m), wombling values (R^2) had a roughly quadratic relationship with spatial covariance: wombling values peaked at approximately 300 m from a boundary (Figure 23). At the 390 x 390 m window size, wombling values peaked at 90 m from a boundary, and wombling values remained consistent at distances > 400 m (Figure 23). Wombling values exhibited a complex relationship with distance to boundaries at the largest window size (990 x 990 m). Wombling values were very low for very far distances (e.g., > 3000 m), then sharply increased to a local peak at 1000 m, then fell, then increased steadily to another peak at 90 m before beginning to decrease at < 90 m from a boundary (Figure 23).

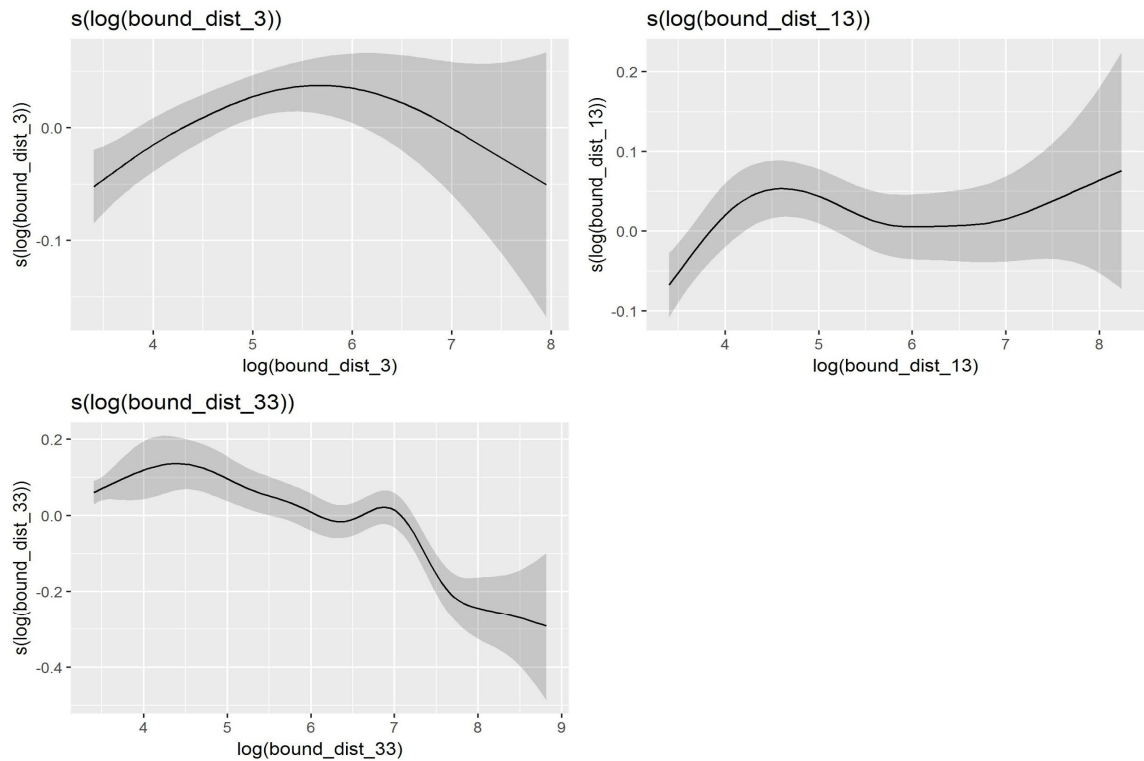


Figure 23. Generalized additive mixed models demonstrate the relationship between spatial regime boundaries derived from a “wombling” method applied to bird community data with distance to known vegetative tree-grassland spatial regime boundaries derived from remotely-sensed spatial covariance. The y-axis depicts the smoothed, predicted relationship between wombling values (R^2) and distance (log-transformed meters) to the nearest spatial regime boundary. Higher wombling values indicate greater likelihood and strength of a boundary.

Wombling predicts changes in spatial regime boundaries

Selected extents

Wombling predicted changing spatial regimes boundaries at selected spatial extents. Where tree regimes were predicted to displace grassland regimes, wombling R^2 values displayed a clear boundary between tree-grassland regimes at the southwest corner of the extent in 1991–prior to

encroachment (Figure 24). As tree regimes displaced grassland regimes over time, wombling values near the shifting spatial regime boundaries responded, increasing and displaying heightened stochasticity (Figure 24). Within the grassland regime that was being displaced, wombling R^2 values were initially low—as expected for values far from a boundary—but began increasing and displaying heightened stochasticity similar to the points nearer the former spatial regime boundary (Figure 24). Interestingly, wombling values within the former “center” of the grassland regime began responding to shifting spatial regime boundaries at > 2 km from encroaching tree spatial regime boundaries (Figure 24).

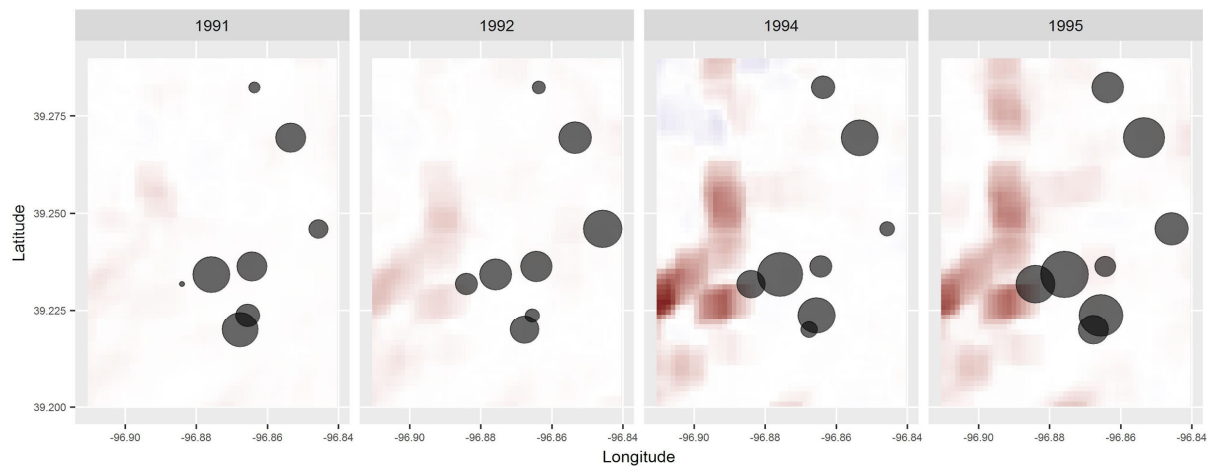


Figure 24. A selected portion of the study area that was likely to exhibit early warnings of changing spatial regime boundaries (regime shifts) due to encroaching tree regimes into grassland regimes. This portion was less disturbed and is near a ravine in which a few trees could have escaped fire and from which tree regimes could expand without fire disturbance. Panels correspond with 4 years in which tree regime boundaries (red shading) rapidly expanded and displaced grassland regimes. Dots indicate bird community sampling locations. Dot size corresponds with wombling (R^2) values, with larger dots indicating greater likelihood of a spatial regime boundary and smaller dots indicating greater similarity lower likelihood of a boundary.)

Where tree-grass regime boundaries were predicted to remain stable due to consistent, heavy fire and military training disturbances, wombling R^2 indeed remained stable over the entire study period (Figure 25). Near the tree-grass boundary, wombling values stayed high, and near the center of the grassland (highly disturbed) regime, wombling values stayed low (Figure 25).

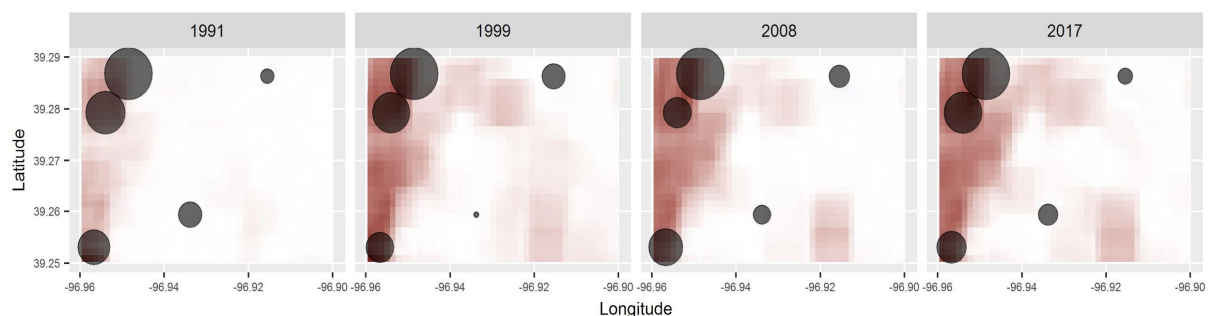


Figure 25. A selected portion of the study area that was likely to have maintained stable tree-grass spatial regime boundaries due to receiving consistent application of fire and being near the center of a grassland

regime. This portion was consistently and heavily disturbed by random and prescribed fires and military training. Panels correspond with 4 years of the 27-year-long study period. Dots indicate bird community sampling locations. Dot size corresponds with wombling (R^2) values, with larger dots indicating greater likelihood of a spatial regime boundary and smaller dots indicating greater similarity lower likelihood of a boundary.

In locations that were initially boundaries between tree-grass regimes and became centers of tree regimes as tree regimes displaced grasslands, in 1991, wombling R^2 values started high at the boundaries, with one point (near the center of the tree regime—that is, in a riparian forest) being markedly low (Figure 26). As tree regimes displaced grassland regimes and boundaries became central, wombling values correspondingly decreased, with all tree-regime points becoming more similar to each other (Figure 26).

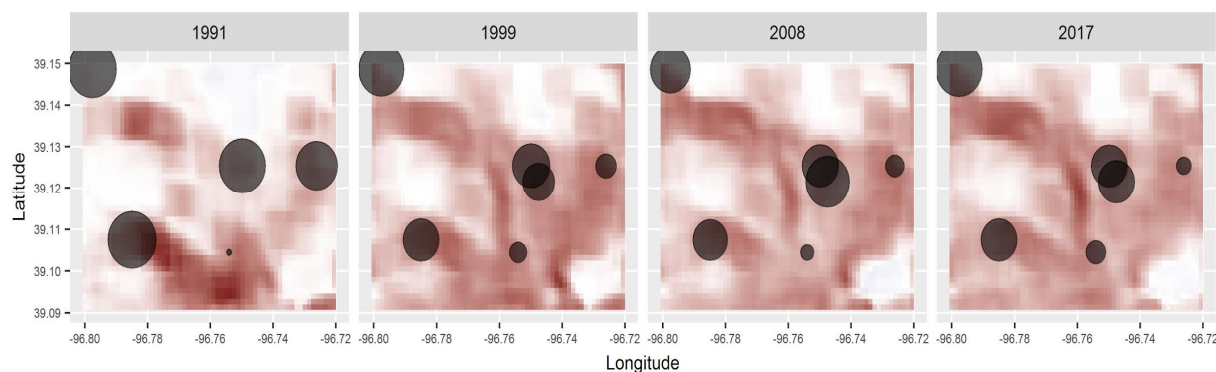


Figure 26. A selected portion of the study area that initially contained a boundary between tree-grass regimes and became centers of tree regimes as tree regimes displaced grasslands. This portion was near a major river that would have historically hosted a tree regime and would have provided a source for tree encroachment of grasslands. Panels correspond with 4 years of the 27-year-long study period. Dots indicate bird community sampling locations. Dot size corresponds with wombling (R^2) values, with larger dots indicating greater likelihood of a spatial regime boundary and smaller dots indicating greater similarity lower likelihood of a boundary.

Within an area highly fragmented by tree-grass regime boundaries, wombling R^2 values reflected that all sampling locations were on or near known vegetative boundaries (Figure 27). Overall, wombling values were high across all sampling locations in the extent. However, as tree regimes further displaced grass regimes and fragmented boundaries drew closer together, wombling values of sampling locations near the center of the extent decreased (Figure 27).

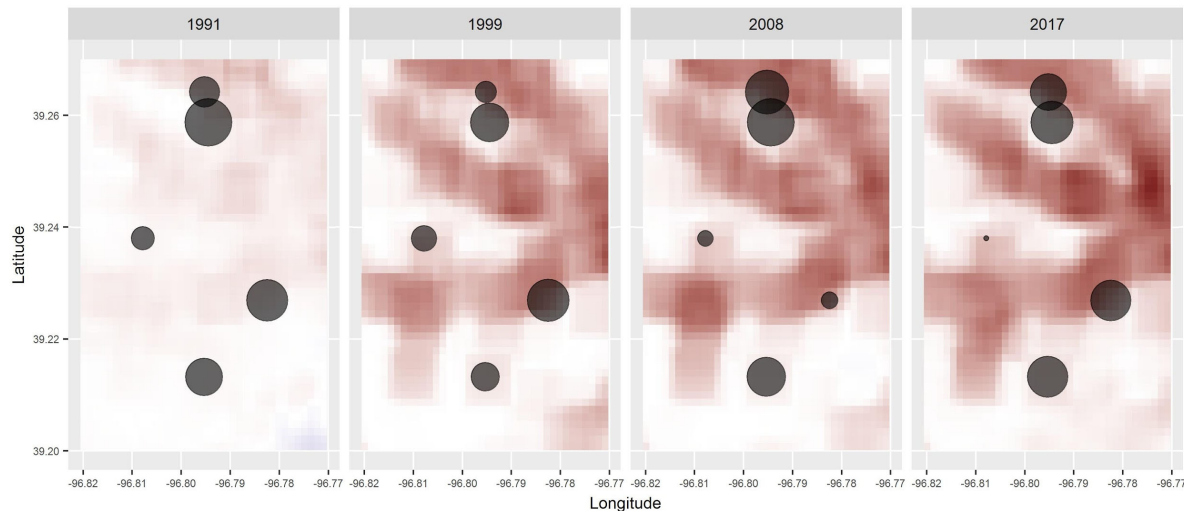


Figure 27. A selected portion of the study area increasingly fragmented by tree-grass regimes. Panels correspond with 4 years of the 27-year-long study period. Dots indicate bird community sampling locations. Dot size corresponds with wombling (R^2) values, with larger dots indicating greater likelihood of a spatial regime boundary and smaller dots indicating greater similarity lower likelihood of a boundary.

Study area extent

At the extent of the entire study area, wombling values displayed complex patterns that tracked patterns in changing vegetative spatial regime boundaries. Overall, wombling R^2 values for sampling locations near the boundaries of the study area (the boundaries of the military installation) tended to be greater than locations nearer the center of the study area. At sampling locations where spatial covariance indicated changing vegetative spatial regime boundaries over time, wombling R^2 values either increased strongly or evidenced stochastic increases and decreases over time. Wombling R^2 values of sampling locations in areas with low spatial covariance (i.e., locations near the center of grassland regimes) tended to be lower and remain lower than locations near tree-grass regime boundaries. Likewise, locations nearer the center of major forested areas (locations near the center of woody plant-dominated regimes) tended to be and remain lower than locations near boundaries. Locations near the more urbanized southern portion of the study area maintained relatively high wombling R^2 values over time.

Discussion

Wombling detected spatial regime boundaries that matched theoretical expectations for a suite of alternative ecological regimes and predicted changes in boundaries of these regimes over time. Wombling predicted regime shifts in space up to 1 km away from known vegetative regime boundaries. These results indicate that wombling represents a major advancement in the detection and prediction of regime shifts. Wombling successfully provided a quantitative, probabilistic method for identifying alternative regimes co-occurring in an open, complex spatial extent (i.e., landscape). Indeed, wombling detected boundaries across a range of spatial regime shift scenarios, including situations in which one regime was clearly being displaced by another as well as situations in which boundaries were less clear and more complex such as highly fragmented areas. Wombling also successfully predicted vulnerability to regime shifts: locations

spatially nearer regime boundaries were more likely to experience (i.e., more vulnerable to) regime shifts than areas farther from boundaries (i.e., near the spatial centers of regimes).

We demonstrate a method for moving regime shift theory and methods beyond mechanistic assumptions and towards embracing complexity theory (C. R. Allen et al., 2016; C. P. Roberts et al., 2018; C. Roberts et al., 2019). Wombling successfully predicted regime shifts with no *a priori* system knowledge and with only the assumption that multiple alternative regimes can coexist in a system (Diniz-Filho et al., 2016). This contrasts with traditional regime shift prediction methods, such as “generic” early warning signals of regime shifts, that make additional mechanistic assumptions, requiring phenomena such as critical slowing down and attendant signals (e.g., rising variance, skewness, kurtosis) to manifest (Burthe et al., 2016; Dakos et al., 2012; Kefi et al., 2014). If fulfilled, these assumptions can provide useful diagnoses of systems undergoing change: for instance, theory predicts that a system exhibiting critical slowing down is reaching a bifurcation point (i.e., not a gradual regime shift or a simple nonlinear transition) (Scheffer & Carpenter, 2003; Van Nes & Scheffer, 2007). But this requires sufficiently long time series data and the manifestation of critical slowing down; and such data and signals are often not obtainable (Clements, Drake, Griffiths, & Ozgul, 2015; Hastings & Wysham, 2010). For example, in our study, we detected a rapid regime shift from a grassland- to tree-regime (Figure that occurred within 5 years. Given our data’s annual time steps and the fact that regime shifts occurred near the beginning of the time steps, early warning and regime shift detection methods would likely have failed to predict a regime shift until after it occurred (Clements et al., 2015; Hastings & Wysham, 2010). In contrast, wombling detected the beginning of the regime shift after a single time step.

Our results align with both resilience theory, which has long acknowledged the scale-dependence of tipping points and scale specificity when considering coexistence of alternative states, and the closely allied Textural Discontinuity Hypothesis, which posits discontinuous breaks in system resource distributions, spatial structures, and organism resource requirements. Bird regimes (wombling-derived boundaries) corresponded with vegetative boundaries at discontinuous scales. Grassland bird species are known to exhibit a variety of responses to tree cover, with some species exhibiting strong aversion to tree cover occurring up to a kilometer away and other species not responding until rather closer, denser tree cover occurs. That discontinuous relationships between bird regime boundaries and vegetative boundaries manifested in spite of idiosyncratic species responses to tree cover further connects our results to and provides support for the Textural Discontinuity Hypothesis and resilience theory.

Wombling also detected areas of self-similarity within regimes, another hallmark of complexity theory and spatial regimes, and wombling showed these areas were near the centers of regimes (C. R. Allen et al., 2016; Sundstrom et al., 2017). We demonstrate this in two situations—when a tree regime is invading a grass regime and a when a tree regime switches from coexisting with grass regimes to being dominant. In both cases, wombling values in the center of regimes were low (i.e., were more self-similar to their neighbors). Additionally, wombling values fell when sampling locations switched from being near boundaries to being closer to the center of a regime, meaning self-similarity can expand alongside regime expansion.

Finally, we show wombling is a promising candidate for applied ecological tasks and research. Without any system knowledge, wombling can provide spatially explicit estimates of vulnerability to regime shifts; that is, locations closer to regime boundaries (high wombling values) would have increased vulnerability (Diniz-Filho et al., 2016; Womble, 1951). In this sense, wombling is applied as a “screening” for regime shift vulnerability—similar to early

warning methods but with fewer assumptions—and local knowledge and post-hoc analyses can be used to further “diagnose” the vulnerability (D. Uden et al., 2019). But if some system knowledge is available for a given landscape (e.g., knowledge of regimes that are desirable vs. undesirable), wombling can both detect emergence and expansion of an undesirable regime or the maintenance and restoration of a desirable regime in a landscape. For instance, we show that wombling detected the emergence and expansion of undesirable tree regimes in a grassland, and we also show that wombling detected the maintenance of a desirable grassland regime when tree-grass boundaries remained stable. It is also important to note that wombling successfully identified boundaries and predicted regime shift vulnerability using a stratified-random sampling design. Future studies should investigate the performance of wombling in simple random or systematic sampling designs.

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Task 6: Synthesis of approaches

Rangeland evaluation and monitoring have been intertwined with advances in ecological theory since the early 20th century (Clements, 1916; Sampson, 1917, 1919). Early successional theory (Clements, 1916) motivated evaluations that linked rangeland degradation to shifts in vegetation following an orderly successional trajectory (Sampson, 1919, 1917; West, 2003). Models of successional retrogression, introduced shortly after coordinated federal monitoring efforts, attempted to provide solutions to the deleterious grazing practices and unrestricted livestock use contributing to widespread soil erosion and increasing dominance of species with lower forage value (Dyksterhuis, 1949). The successional retrogression model dominated rangeland management for 50 years, until advances in alternative state theory and the inability of the succession-retrogression model to explain many changes in rangelands prompted a shift to the state-and-transition modeling framework introduced by Westoby et al. (1989). State-and-transition models are one of the most commonly-used management frameworks in the world (i.e., USDA Ecological Site Descriptions State-and-Transition Models), but capture only a small component of the complex, adaptive behaviors that ultimately determine why ecosystems persist or, alternatively, change form (Twidwell et al., 2013).

New concepts have emerged in theoretical ecology with the intent to not only quantify complexities in ecological change inherently unaccounted for in state-and-transition models but to also help applied ecologists "turn back from the brink" prior to reaching regime shifts (i.e., state transitions; definitions provided in Table 7) in ecological systems (Biggs et al., 2009). These concepts center around the theory that ecological systems can exist in multiple, dynamic basins of attraction (i.e. regimes), fundamentally similar to "states" of the state-and-transition models (Briske et al., 2008; Scheffer, 2003). Overwhelming disturbance(s) can push a regime past a threshold and into an alternate regime (Briske et al., 2005; Folke et al., 2004; Scheffer and Carpenter, 2003). Systems that have undergone shifts to regimes with lower ecosystem service potential (e.g., desertification or woody encroachment of rangelands) may exhibit hysteretic behavior; that is, restoration to the previous regime would require more effort than if it had been initiated prior to the regime shift, or the restoration would be practically infeasible (Angeler and Allen, 2016; Folke et al., 2004; Scheffer et al., 2001). Using metrics that signal early warning indicators (EWIs) and avoid regime shifts that are undesirable have therefore become a central pursuit in ecology (Andersen et al., 2009; Brock and Carpenter, 2012, 2006; Dakos et al., 2012), especially for known regime changes that exhibit strong hysteretic behavior. Theoretical ecologists have explored the behavior of state variables in systems on the cusp of regime shifts or where regime shifts were known *a priori* (Carpenter et al., 2011; Mantua, 2004). Much work has been done to assess early warning signals of regime shifts with univariate data and simple model systems (Burthe et al., 2015); however, univariate indicators may not capture the true complexity of ecosystem change possible with multivariate methods (Allen and Holling, 2008; Eason et al., 2016; Rodionov, 2004; Spanbauer et al., 2014).

Table 7. Glossary of terms.

Term	Definition
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Early Warning Indicator	"hypothesized to signal the loss of system resilience and have been shown to precede critical transitions in theoretical models, paleoclimate times series, and in laboratory as well as whole lake experiments" (Gsell et al. 2016)
Hysteresis	"in which the forward and backward switches occur at different critical conditions" (Scheffer et al. 2001) "the path out is not the same as the path in" (Angeler and Allen 2016)
Regime	"configuration in terms of abundance and composition, function and process, of a system...The terms state and regime are often used interchangeably. However, regime specifically refers to the processes and feedbacks that confer dynamic structure to a given state of a system" (Angeler and Allen 2016)
Regime Shift	"conspicuous jumps from one rather stable [regime] to another" (Scheffer et al. 2001) "Sudden shifts in ecosystems, whereby a threshold is passed and the core functions, structure, and processes of the new regime are fundamentally different from the previous regime and hysteresis is present." (Scheffer and Carpenter 2003)
Regime Shift Metric	"statistical metrics of system resilience [that] have been hypothesized to provide advance warning of sudden shifts in ecosystems" (Gsell et al. 2016)
State	"The 'state' of a system at a particular instant in time is the collection of values of the 'state' variables at that time...the term 'state' is loosely used to describe a characteristic of the system, rather than its state. For example, the lake is in a eutrophic 'state', or the rangeland is in a shrub-dominated 'state'." (Walker et al. 2002)
State-and-Transition Models	"...a framework to accommodate a broader spectrum of vegetation dynamics on the basis of managerial, rather than ecological, criteria... initially designed for application on rangelands characterized by discontinuous and nonreversible vegetation dynamics." Based on "1) potential alternative vegetation states [at] a site, 2) potential transitions between vegetation states, and 3) recognition of opportunities to achieve favorable transitions and hazards to avoid unfavorable transitions between vegetation states" (Briske et al. 2005)
State Variable	Biotic and abiotic system features that define and contrast system states. State variables can be "driving state variables" of system states (i.e., sufficient changes in driving state variables are known to alter system states) or simply indicative of system state.
Threshold	"Thresholds are equivalent to tipping points and may be detected as discontinuities or bifurcation points in complex systems" (Angeler and Allen 2016)

The rangeland discipline, given its emphasis on long-term multivariate experimentation and monitoring programs that occur across multiple spatial and temporal scales, is poised to uniquely contribute to the science of early warnings and regime shifts in ecology. Theoretical ecology will benefit from the myriad of multivariate monitoring data available in rangelands to continue the tradition in rangelands of empirically testing new ideas associated with ecological assembly (Briske et al., 2005). The rangeland discipline will also benefit from merging convergent theoretical ecology concepts and techniques aimed at quantifying state transitions

and providing a quantitative basis for making decisions in rangeland management (Allen et al., 2016; Angeler and Allen, 2016). But despite the applicability of early warning and regime shift theory to rangeland science, evidence suggests that rangeland science is lagging in the assessment of theoretical indicators used for regime shift prediction (Table 8). To date, most rangeland research has focused on qualitative assessments of state transitions, as opposed to quantitative and predictive metrics (Bestelmeyer et al., 2009; Twidwell et al., 2013; but see Bashari et al. 2008; Table 8).

Table 8. Literature review[†] of the total number of papers and the percentage using a quantitative metric[‡] for early warning and regime shift detection in Rangeland Ecology & Management and other journals in the discipline.

Search term	In the journal of Rangeland Ecology & Management	In other journals in the discipline with the additional search term:	
		Rangeland	Ecology
State and Transition	147 (21%)	2,250 (30%)	3,450 (27%)
Alternative States	36 (31%)	953 (32%)	5,690 (30%)
State Transition	24 (17%)	580 (35%)	8,470 (30%)
Early Warning	18 (17%)	5,340 (26%)	17,500 (71%)
Regime Shift	7 (29%)	672 (42%)	110,000 (46%)
Early Warning Indicator	2 (0%)	87 (61%)	1,000 (42%)
Spatial Regime	0 (0%)	9 (33%)	310 (68%)

[†]Search returns were based on a formal review in Google Scholar. Values given in the table represent the sum of all search returns. Values in parentheses represent the percentage (%) of search returns including a quantitative metric.

[‡]Quantitative metrics considered in our search include: autocorrelation, autoregressive model, autoregressive moving averages, average standard deviates, BDS test, coefficient of variation, conditional heteroscedasticity, conditional probability analysis, detrended canonical correspondence analysis, detrended correspondence analysis, detrended fluctuation analysis indicator, discontinuity analysis, fisher information, generalized modeling, intervention analysis, kurtosis, return rate, sequential T-test analysis of regime shifts, skewness, spectral density, spectral exponent, spectral ratio, standard deviation, vector autoregressive modeling.

In this paper, we review and discuss multivariate metrics used to detect early warnings and regime shifts along with their utility in rangeland evaluation and monitoring. We focus on multivariate metrics with potential utility for detecting rangelands in transition, as opposed to univariate indicators, because the rangeland discipline has a long history of multivariate data inventory and monitoring, and comprehensive reviews of univariate metrics already exist that can guide rangeland specialists (e.g., Dakos et al., 2012). For each metric, we review the conceptual foundation leading to its proposed use as an early warning indicator of system-level

change, highlight known shortcomings, and identify specific situations where each metric will be most useful for rangeland science, monitoring, and management. A suite of multivariate-based early warning and regime shift indicators were reviewed in this paper and provide a broad range of potential metrics applicable to a wide variety of data types and contexts – from situations where a great deal is known about the key system drivers and a regime shift is *a priori* hypothesized, to situations where the key drivers and the possibility of a regime shift are both unknown. We then provide three examples that showcase the potential utility of these metrics to future pursuits in rangeland science and management.

Literature review and methodology

We conducted a formal review using Web of Science to compile different multivariate metrics used for early warning and regime shift detection (Web of Science 2016; accessed on January 2016 - June 2016). Accordingly, we used the following search terms: "Regime Shift AND Multivariate AND Each Metric Type".

We found 70 articles that used multivariate early warning and regime shift metrics in ecological studies. In these articles, we found ten unique metrics, with the number of articles using each metric varying from 1 - 14 (Average Standard Deviates = 4, Conditional Probability Analysis = 1, Detrended Correspondence/Detrended Canonical Correspondence Analysis = 11, Discontinuity Analysis = 4, Fisher Information = 14, Generalized Modeling = 2, Intervention Analysis/Autoregressive Moving Averages = 5, Redundancy Analysis-distance-based Moran's Eigenvector Map/Asymmetric Eigenvector Map = 11, Sequential T-test Analysis of Regime Shifts = 14, Vector Autoregressive Model = 4). Three metrics had been tested as EWI metrics (Conditional Probability Analysis, Discontinuity Analysis, Fisher Information), and the rest were regime shift detection metrics that have the potential to be or have been proposed as EWI metrics. Thus, we hereafter distinguish between "tested" and "proposed" EWI metrics. The earliest application of multivariate EWI metrics was in the early 1990's (Ebbesmeyer et al., 1991), and their use sharply increased beginning in the early 2000's (Web of Science 2016). Most studies we found used EWI metrics for time-series and aquatic system applications (Kirkman et al., 2015; Mantua, 2004), with only two studies using EWI metrics to detect regime shifts in space or terrestrial systems (Sundstrom et al., 2017; Zurlini et al., 2014).

To assist in the appropriate selection and application of multivariate EWI metrics in rangeland applications, we categorized metrics hierarchically according to their assumptions and data type requirements (Figure 28) and organized the review accordingly. The primary division lies in whether driving state variables are known or unknown for the system in question (Table 3) and whether a relatively small (i.e., limited), or a relatively large (i.e., unlimited) number of state variables have been measured (Figure 28). The second division separates metrics by whether they require the spatial or temporal "location" of a regime shift to be hypothesized *a priori* (Figure 28). The tertiary division splits metrics by specific data type requirements (Figure 28).

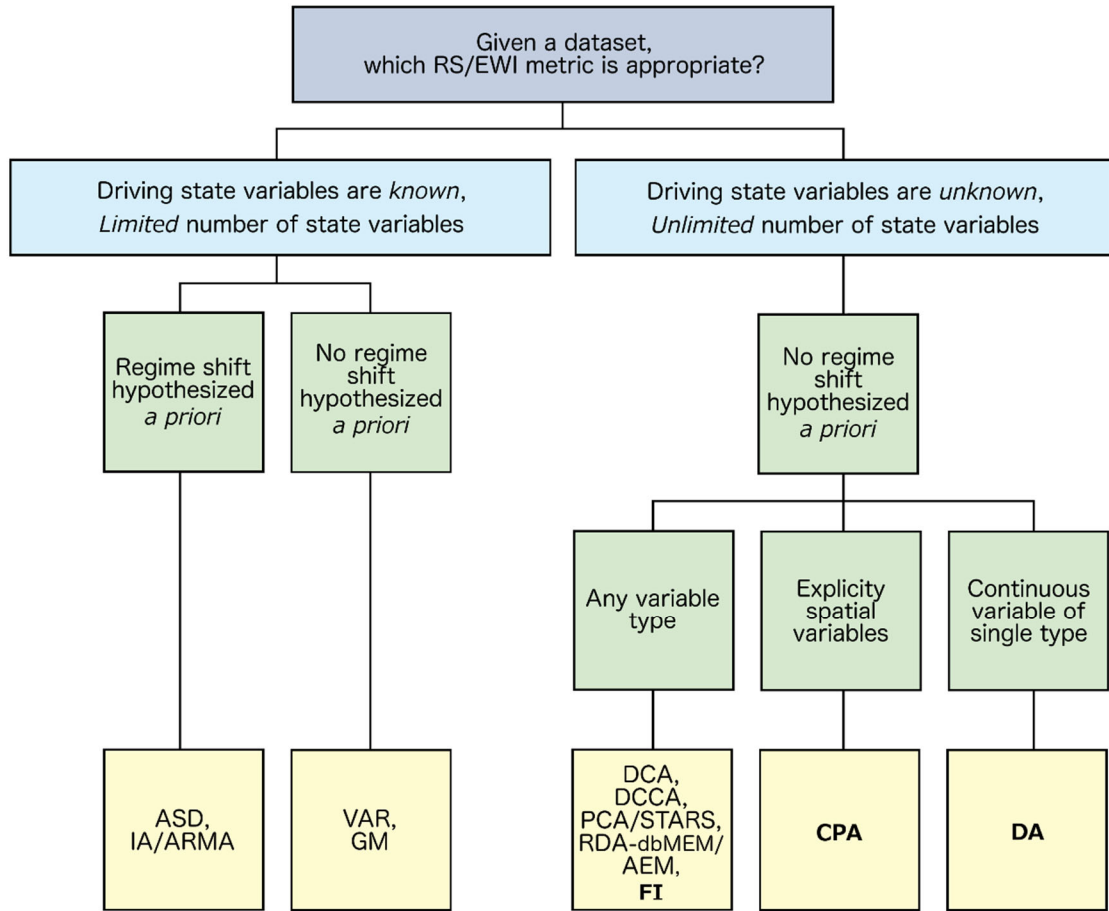


Figure 28. A flowchart for determining which multivariate metrics for regime shift/early warning detection are appropriate for a given set of state variables. “Limited” state variables indicates those metrics are suitable for relatively small number of input variables, and “known drivers” means that the input state variables represent known fundamental influences on system state. The lowest tier lists appropriate metrics for a given data type. Metrics in bold have been tested as early warning indicators of regime shifts. Metrics not in bold have been proposed as early warning metrics but only tested as regime shift indicators. *Note:* RS = proposed early warning indicator, EWI = tested early warning indicator, ASD = Average Standard Deviates, IA/ARMA = Intervention Analysis/Autoregressive Moving Averages, VAR = Vector Autoregression, GM = Generalized Modeling, DCA = Detrended Correspondence Analysis, DCCA = Detrended Canonical Correspondence Analysis, PCA/STARS = Principal Components Analysis/Sequential T-Test Analysis of Regime Shifts, RDA-dbMEM/AEM = Redundancy Analysis-, FI = Fisher Information, CPA = Conditional Probability Analysis, DA = Discontinuity Analysis.

Synthesis of metrics

Known driving state variables/Limited number of state variables

Metrics in this division (known/limited) share two assumptions: driving state variables are known, and driving state variables interact with each other (Fig. 1). Known/limited metrics all use regression-like methods, estimate coefficients, and have implicit significance tests (e.g.,

Solow and Beet, 2005; Lade and Gross, 2012), making them similar to non-linear threshold modeling techniques (Sasaki et al., 2008). For these metrics, the regime is defined by modeling the interactions and variability amongst the chosen state variables, and a regime shift is detected when the behavior of state variables deviate significantly from a "typical" range at a given level of confidence (Gal and Anderson, 2010; Lade et al., 2013). Two of the known/limited metrics require *a priori* hypotheses of regime shift locations (Average Standard Deviates, Intervention Analysis/Autoregressive Moving Averages), and two known/limited metrics do not require *a priori* regime shift hypotheses (Vector Autoregression, Generalized Modeling). Known/limited metrics that do not require a regime shift to be hypothesized *a priori* can potentially provide early warnings if trends in state variable behavior approach the given confidence limit (Ives and Dakos, 2012).

These metrics can provide detailed quantitative and statistically rigorous results, but they require substantial system-specific *a priori* knowledge (Gal and Anderson, 2010; Rudnick and Davis, 2003). Major benefits of known/limited metrics include: (1) their ability to assess the validity of regime shifts and early warnings via null hypothesis tests and information theoretic approaches and (2) their ability to estimate the directionality and relative importance of the chosen driving state variables via coefficient estimation (Gal and Anderson, 2010; Lade and Gross, 2012). Because known/limited metrics assume driving state variables are known, correctly selecting state variables is essential (Solow and Beet, 2005). Not including major driving variables or analyzing irrelevant variables could produce biased estimates or fail to detect regime shifts (Hare and Mantua, 2000). Additionally, overly conservative confidence requirements or biased estimates of "typical" ranges of state variable behavior may cause regime shift detection to lag (Ives and Dakos, 2012).

Regime shift hypothesized a priori

Average Standard Deviates

Average Standard Deviates (ASD), developed by Ebbesmeyer et al. (1991), is a proposed EWI metric that focuses on identifying significant regime shifts using the magnitude of change in multiple time series records between pre- and post- *a priori* identified regime shift dates. Hare and Mantua (2000), Rudnick and Davis (2003), and Mantua (2004) summarize the methods in detail. Regime shifts are considered significant if the sign of standard deviates in all years is the same within each "half record" (designated by the location of the *a priori* identified step change) but opposite between half records, and no value is within a standard error of zero. This method has been strongly contested by Rudnick and Davis (2003), who remark on how it is designed to specifically create a step change and is highly sensitive to false positives when there is noise in the data. Mantua (2004) suggests an alternative method to mitigate this weakness, but to our knowledge, this has not been assessed within ecological regime shift literature. As of this review, ASD has been used solely in marine environments (Mantua, 2004).

Intervention Analysis/Autoregressive Moving Averages

Intervention analysis (IA; Wei, 1994) combined with autoregressive moving averages (ARMA) is a paired method for detecting significant changes in the mean of state variables in a time series while accounting for temporal autocorrelation (Andersen et al., 2009; Mantua, 2004). Together, intervention analysis and autoregressive moving average models (IA/ARMA) have been used to estimate the significance and magnitude of regime shifts in time series data (Gedalof et al., 2001). IA/ARMA requires either *a priori* knowledge of the regime shift (intervention) or an estimate of the temporal location of the shift, which can be identified by visual inspection of the time series data (Mantua, 2004). Intervention analysis is a method for confirming the presence of a regime shift on time series data, and ARMA is used in combination with IA when temporal autocorrelation is present or suspected in the data. Although IA accounts for stochastic noise, it may provide more useful knowledge about a system when using detrended data (Mantua, 2004).

No regime shift hypothesized a priori

Vector Autoregressive Model

Vector Autoregressive Modeling (VAR) models interactions between state variables and estimates coefficients much like a least squares regression (Mantua, 2004) and identifies regime shifts as switches from locally steady states in fitted values (Gal and Anderson, 2010). A parametric bootstrapping technique can determine statistical significance of changes in fitted values, and Markov-switching techniques can be added (Gal and Anderson, 2010). VAR has been applied to time-series data in aquatic systems and simulated data (Gal and Anderson, 2010; Mantua, 2004; Solow and Beet, 2005; Ives and Dakos, 2012). VAR can detect unknown (not hypothesized *a priori*) regime shifts and accounts for autocorrelation between variables and observations (Ives and Dakos, 2012). VAR cannot detect a regime shift in the first or last observation of a time-series, potentially causing lagged early warnings of regime shifts (Gal and Anderson, 2010). However, fitted values approaching the limit of the typical range of variability in a system could still provide an early warning signal (Ives and Dakos, 2012).

Generalized Modeling

Introduced by Lade and Gross (2012), generalized modeling (GM) as a proposed EWI metric creates dynamical functions to describe each variable and their interactions with other variables. Across a macroscopic time-scale, certain variables are assumed to change rapidly and stochastically around a locally stable state ("fast" variables), whereas others change gradually ("slow variables"). GM detects early warnings or regime shifts when eigenvalues in the "fast" variables shift away from their locally-stable state (Lade and Gross, 2012). The GM metric is advantageous in that it requires relatively few time-series data points to robustly detect early warnings or regime shifts (Lade and Gross, 2012; Lade et al., 2013), and it can account for stochastic fluctuations in fast variables (Lade and Gross, 2012). However, high levels of noise in fast variables are known to decrease the accuracy of regime shift detection (Lade and Gross,

2012). Although GM has received little rigorous statistical testing in ecology, it shares many potential applications with the VAR metric (Lade and Gross, 2012).

Known OR unknown driving state variables/Unlimited number of state variables

Overall, metrics in this division (unknown/unlimited) have fewer assumptions than the previous division (Angeler and Johnson, 2012; Spanbauer et al., 2016; Fig. 1). They do not require *a priori* knowledge about which state variables drive system form and function (although known driving state variables can be used), can readily accept an unlimited number of state variable inputs, and do not require *a priori* hypotheses of the spatial or temporal locations of regime shifts (Carstensen et al., 2013; Eason et al., 2016; Rodionov, 2004; Sundstrom et al., 2017; Zurlini et al., 2014). However, a few unknown/unlimited metrics have specific data type requirements, which produce tertiary divisions (Fig. 1). Metrics that accept any type or combination of state variables (Sequential T-test Analysis of Regime Shifts, Detrended Correspondence Analysis, Detrended Canonical Correspondence Analysis, Redundancy Analysis/distance-based Moran Eigenvector Maps or Asymmetric Eigenvector Maps, Fisher Information) define regimes by condensing state variables into a single value as a series of data points (e.g. a time-series, a spatial transect). These values fall within a stable range of variability, and regime shifts occur when values exceed a pre-determined range of variability (e.g., Karunanithi et al., 2011; Baho et al., 2014). Discontinuity analysis, identifies gaps, or scale-breaks, in continuous, rank-ordered data of a single type (Allen and Holling, 2008). Finally, Conditional Probability Analysis requires explicitly spatial data to detect shifts in cross-scale spatial state variable connectivity (Zurlini et al., 2014).

Major advantages of unknown/unlimited metrics include their flexibility and the fact that three have been tested for EWI applications (Fisher Information, Discontinuity Analysis, Conditional Probability Analysis; Fig. 1). Additionally, these metrics can consider an unlimited number of state variables and combinations of data types (except for Discontinuity Analysis and Conditional Probability Analysis—see below; Fig. 1), and they require little to no *a priori* system knowledge (Mayer et al., 2007; Tian et al., 2008). Some of these metrics are also capable of significance tests or information theoretic model selection (e.g., Detrended Correspondence Analysis, Detrended Canonical Correspondence Analysis, Sequential T-test Analysis of Regime Shifts, Redundancy Analysis-distance-based Moran's Eigenvector Maps/Asymmetric Eigenvector Maps; Rodionov and Overland, 2005), but unlike known/limited metrics, they do not estimate coefficients, meaning significance tests for unknown/unlimited metrics may produce less specific conclusions than other approaches (Baho et al., 2014; Rodionov, 2004). However, the ability to include unlimited state variables may lead to including extraneous variables that could in turn lead to spurious regime shift detections (Sundstrom et al., 2012). Also, because these metrics do not require input state variables to be drivers or to interact, they provide little information on the directionality or relative importance of state variables regarding regime shifts (Vance et al., 2015).

Any variable type

Fisher Information

Fisher Information (FI) is a tested EWI metric, and previous applications demonstrate its utility for early warning detection, regime shift detection, and land management decisions (A.M. González-Mejía, 2015; Eason et al., 2016; Sundstrom et al., 2017). FI is a measure of the amount of information surrounding an unknown parameter that is obtainable by observation (Fisher, 1922). It is rooted in statistical estimation theory and has been applied in variety of disciplines ranging from quantum mechanics to ecosystem dynamics (Fath and Cabezas, 2004; Frieden and Gatenby, 2010; Mayer et al., 2007; Pawlowski et al., 2005). FI was recently adapted to assess changes in system behavior and detect regime shifts in complex ecological and social ecological systems (Eason et al., 2012; Fath et al., 2003; González-Mejía et al., 2014; Karunanithi et al., 2011; Sundstrom et al., 2017; Vance et al., 2015). As a measure of overall system order, FI defines regimes as steady or increasing order and regime shifts as sudden losses of order (Eason et al., 2014; Mayer et al., 2007). Losses of order occur when state variables exceed their typical range of variability (Eason et al., 2016; Spanbauer et al., 2014). In addition to advantages shared with other unknown/unlimited metrics, FI can detect regime shifts and early warnings regardless of resolution or length of the data set (Eason et al., 2016; Spanbauer et al., 2014). For example, Spanbauer et al. (2014) applied FI to a time series dataset on over 100 species of freshwater diatoms across > 7,000 year period and found evidence of long term instability preceding a regime shift in community structure. Although FI has primarily been used to assess temporal dynamics, Sundstrom et al. (2017) also used this method to detect regime shifts in space (i.e., spatial regime boundaries) in terrestrial and aquatic community data. Researchers have used FI with other approaches including the variance index (Carpenter and Brock, 2006; Sundstrom et al., 2017) and discontinuity analysis (Spanbauer et al., 2016).

Sequential T-Test Analysis of Regime Shifts

Sequential T-Test Analysis of Regime Shifts (STARS) was initially proposed by Rodionov (2004) as a method for testing for the occurrence of climatic regime shifts. STARS can provide early warning indicators of a regime shift via formal statistical significance tests by using a sequential data processing technique that allows for exploratory analysis that is not dependent on *a priori* hypothesis for locating regime shifts (Rodionov, 2004). STARS has been applied to a range of time series data beyond climate, including invertebrate and vertebrate community composition data (Chiba et al., 2009; Kirkman et al., 2015; Tian et al., 2008; Wood and Austin, 2009), snowpack characteristics (Irannezhad et al., 2015), streamflow (Johnston and Shmagin, 2008), sea surface temperature (Friedland and Hare, 2007) and thermohaline characteristics (Matić et al., 2011). This method works well in collaboration with variable reduction techniques such as Principal Components Analysis, allowing for the inclusion of a large range of climatic, environmental and ecological data categories (McQuatters-Gollop and Vermaat, 2011).

Detrended Correspondence Analysis & Detrended Canonical Correspondence Analysis

Detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) are two multivariate ordination methods typically used on sparse ecological data (Ter Braak, 1986), often where ecological community assemblage data on species with normal distributions with respect to environmental gradients need to be detrended (remove arch effects; Hill and Gauch Jr, 1980). DCA and DCCA have been used as regime shift detection methods by searching for flickering, skewness, and autocorrelation of variance over time in community or assemblage diversity and structure (Carstensen et al., 2013). For instance, by using a single ordinated axis, DCA identified a livestock grazing threshold gradient and possible regime shift on rangeland plant communities (Sasaki et al., 2008), and DCCA has been used to estimate historic diatom Beta diversity (Hobbs et al., 2010; Liu et al., 2013). DCCA and DCA may be less reliable in detecting changes in systems if the response variable does not follow a Gaussian distribution (Ter Braak, 1986).

Redundancy Analysis – distance-based Moran’s Eigenvector Maps/Asymmetric Eigenvector Maps

Redundancy Analysis (RDA)-distance-based Moran’s Eigenvector Maps/Asymmetric Eigenvector Maps (dbMEM/AEM) is a proposed EWI metric that detects regime shifts and changes in ecological structure by identifying ecological patterns at different spatial or temporal scales; that is, it disentangles decadal, interannual, seasonal and intraseasonal patterns in time series or continental, regional and local patterns in data (Angeler et al., 2009; Borcard and Legendre, 2002; Borcard et al., 2004). A refinement of the principal coordinate of neighbor matrix approach, this metric instead uses RDA and models space or time with a dbMEM or dbAEM approach (Angeler et al., 2009; Dray et al., 2006). Rather than using spatial coordinates or a linear time vector directly, dbMEM and AEM carry out a fourier transformation to spectrally decompose the spatial/temporal relationships among data points into orthogonal eigenfunctions. The resulting functions look like sine waves (or distorted sine waves if the sampling is irregular) of distinct frequencies that are then used as predictor variables in the RDA (Angeler et al., 2010). The number and structure of predictor variables obtained for analysis depends on the length/spatial extent and resolution/grain of the underlying data set. dbMEM differs from AEM in that the latter includes a linear vector in addition to the sine waves, which allows modeling unidirectional processes in time and space (e.g., hydrological flow in streams; Baho et al., 2014; Göthe et al., 2014). The RDA-dbMEM/AEM methods uses rigorous permutation testing, allowing for the determination of robust patterns and numerical assessment of the relative importance of patterns detected at each scale using the amount of adjusted variance explained. This metric has been used in both spatial and temporal contexts with data from lakes and streams (Angeler et al., 2014), marine systems (e.g., Angeler et al., 2014), ancient aquatic systems (Spanbauer et al. 2014), and terrestrial ecosystems (e.g., Widenfalk et al., 2016). These analyses often focus on assessing the organization of the complex behavior and resilience of these systems and their application in management (Angeler and Allen, 2016).

Continuous variables of the same Type

Discontinuity Analysis

Discontinuity analysis (DA) is a method developed to objectively identify discontinuities, or scale breaks, in rank-ordered data, and it has been tested as an EWI metric (Allen and Holling, 2008; Nash et al., 2014; Spanbauer et al. 2016; Sundstrom et al., 2012). DA arises from ecological theory that posits ecosystems are multi-scaled and hierarchical as a result of structuring processes operating over discrete ranges of spatial and temporal scales (Allen and Starr, 1982; Holling, 1992). Both ecological structure and the species that interact with that structure are scaled in the sense that they function within a limited and particular range of spatial and temporal scales (Allen and Holling, 2008). Animal body masses, which are highly allometric with life-history traits, fall into size classes detectable by DA and can be used as a proxy for the complex spatial and temporal scales of ecological structure and structuring processes (Nash et al., 2014). Changes in body mass size classes in a system over time or space can therefore suggest changes in ecological regimes when regime shifts represent shifts in basic ecological structuring processes (Peterson et al., 1998). For example, used in conjunction with constrained hierarchical clustering, DA detected early warnings of regime shifts in paleodiatom data in freshwater lakes by identifying shifts in the number and location of diatom body mass discontinuities (Spanbauer et al., 2016). DA also detected simplified fish size classes in degraded coral reefs compared to healthier reefs (Nash et al., 2013).

Explicitly spatial variables

Conditional Probability Analysis

Conditional Probability Analysis (CPA) uses explicitly spatial data to detect regime shifts by assessing changes in spatial cross-scale land use-land cover connectivity (Zurlini et al., 2014). Using multiple spatial data layers, it calculates proportional land use-land cover (P_c) and connectivity (i.e. adjacency; P_{cc}) within moving spatial windows of various sizes. As P_c of a given land use-land cover type increases, P_{cc} increases steadily until a threshold point is breached. At this threshold, a regime shift occurs: as a new land use-land cover regime spreads, P_c abruptly increases exponentially and P_{cc} increases much more slowly. In the single study we found using CPA, the authors detected an early warning of a regime shift toward desertification as a result of increased agricultural land connectivity in an urban-rural region of southern Italy (Zurlini et al., 2014).

Discussion

The range science discipline has one of the longest histories of using large-scale rangeland inventories and analyses to influence major land management decisions and to avoid alternative ecological regimes with less ecosystem service potential (West, 2003). In North America, the first well-coordinated national inventory of terrestrial resources occurred in the US in 1934 to address concerns over ecological transformations due to soil erosion (National Erosion Reconnaissance Survey). In the decades following, US land management agencies have

launched multiple inventory frameworks aimed at maintaining favorable conditions and preventing deleterious regime shifts such as monitoring range quality, estimating degree of rangeland degradation, maintaining so-called climax communities, and tracking the degree of invasion by exotic species (West, 2003). But although monitoring efforts have been successful at identifying ecosystem changes after their occurrence, they often rely on subjective expert opinion or system-specific knowledge applied after the fact, thereby removing the ability to predict emergent, unexpected change inevitable in ecological systems (Twidwell et al., 2013).

The early warning and regime shift detection metrics we review are meant to avoid problems associated with subjectivity and system-specific knowledge requirements. These metrics are often specifically designed to predict surprise and can be applied to presently available rangeland monitoring inventories to directly answer rangeland management and state-transition concerns in a spatially-explicit manner. While spatial regime metrics have not undergone robust experimental evaluation in ecology and even less in the rangeland discipline (Table 8), many robust multivariate rangeland datasets have potential for testing and applying the early warning indicators that can be applied to multivariate data (e.g., the Natural Resources Conservation Service's "Natural Resources Inventory", the US Forest Service's "Forest Inventory and Analysis Program", the US Department of Agriculture's Animal and Plant Health Inspection Service's "Mormon Cricket/Grasshopper Assessment Program"; USDA NRCS, 2015; USDA Forest Service, 2018; USDA APHIS, 2018). For instance, the generalizability of unknown/unlimited metrics such as Fisher Information or Sequential T-test Analysis of Regime Shifts makes them amenable for use in surveillance monitoring frameworks that collect broad swathes of data of various types and any state variable could be of interest (Hutto et al. 2012). Additionally, some unknown/unlimited metrics like RDA-dbMEM/AEM and Discontinuity Analysis have the potential to identify regime shifts and early warning while also estimating the complexity and resilience of rangelands—thereby providing more detailed information on the state of the system and potentially how close or far it is from a regime shift. Conversely, sites with long-term monitoring (e.g., Long-Term Ecological Research (LTER) sites, Department of Defense lands, or individual properties) or where long-term data might be available in the future, and where the drivers are known (e.g. percent cover of woody plants at Konza Prairie LTER, bare ground at Jornada Basin LTER; Jornada Basin LTER, 2018; Konza Prairie LTER, 2018), known/limited metrics have high potential for early warning applications, depending on how data were collected. For instance, fitted values for percent bare ground at Jornada Basin flickering outside "typical" range of variability or consistently moving toward the boundaries of the typical range of variability could represent early warnings of a state transition (Dakos et al., 2012; Ives and Dakos, 2012; Solow and Beet, 2005). Similarly, EW metrics requiring hypothesized regime shift locations (e.g., Average Standard Deviates, Intervention Analysis/Autoregressive Moving Averages) can be used in a post-hoc manner with long-term data, and they could also potentially be turned to produce early warnings by sequentially hypothesizing regime shifts in time series data. EW metrics can also be used to detect regime shifts in spatial rangeland datasets (i.e., as has been assessed with Fisher Information for breeding bird data; Sundstrom et al., 2017).

The new concept of spatial regimes brings together early warning, regime shift, and state-transition theories by identifying where ecological regime shifts/state-transitions are taking place

in space and time. Derived from regime shift and alternative state theory, spatial regimes are defined as spatially explicit ecological systems maintained by feedback mechanisms that exhibit self-similarity in structure and composition within their boundaries (Allen et al., 2016; Sundstrom et al. 2017). The abundance of spatial data for rangelands (e.g., remotely-sensed vegetation indices, fire history data, land use-land cover data), the geographic breadth of monitoring sites (e.g., the NRCS Natural Resources Inventory's sites distributed throughout private agricultural lands across the United States), and the geographic site-descriptive goals of many rangeland initiatives (e.g., Ecological Site Descriptions) suggest high potential for applying the spatial regime concept in conjunction with EWI metrics in rangelands. For instance, we report only a single article using an EWI metric in a spatial regime context (Sundstrom et al. 2017) and none in rangelands (Table 8), but other EWI metrics with similar approaches to Fisher Information (e.g., Sequential T-test Analysis of Regime Shifts, Discontinuity Analysis) could also be used for spatial regime detection on large-scale (e.g., the US Geological Survey's "North American Breeding Bird Survey") or local-scale (e.g., georeferenced Long-Term Ecological Research site) datasets. Likewise, Conditional Probability Analysis, as a tested EWI metric that requires explicitly spatial data, could potentially be used to detect spatial regimes via cross-scale connectivity in remotely-sensed rangeland data, searching for early warnings in loss of rangeland heterogeneity, for signs of fragmentation, or for signs of over-connectedness and rigidity traps (Fuhlendorf and Engle, 2001; Hobbs et al., 2008; Peters et al., 2015; Zurlini et al., 2014).

Ignoring the interaction between space and time when searching for patterns indicating early warnings and regime shifts can lead to ecological misinterpretations of underlying structure of state variables (Allen et al., 2014; Baho et al., 2015; Nash et al., 2014). For instance, temporal early warnings of regime shifts in yeast populations were found to be suppressed in systems with high levels of connectivity, suggesting that EWI performance is jeopardized by ignoring integrated spatial-temporal components (Dai, 2013). To incorporate interactions between scale-specific spatial and temporal processes into early warning and regime shift modeling, approaches such as spatial/temporal eigenfunction analyses (e.g. the RDA-dbMEM/AEM metric reviewed above; Blanchet et al., 2008) have arisen to identify characteristic spatial and temporal scales at which processes act to structure the distribution of species in a community (Dray et al., 2006, 2012; Peres-Neto and Legendre, 2010; Smith and Lundholm, 2010). Often spatial/temporal eigenvectors are combined with canonical ordination techniques or other multivariate community models to account for spatial-temporal patterns in community data, thereby offering increased performance for detecting regime shifts in systems where there is strong coupling of spatial and temporal variation at multiple scales (Legendre and Gauthier, 2014). Although many EWI metrics do not, spatial/temporal eigenfunction analyses often require large-scale and/or long-term data relative to the community of interest, making the intensive monitoring data collected by rangeland scientists and managers imperative for using these EWI metrics and disentangling spatiotemporal scaling issues.

To identify situations when EWI metrics would be useful and appropriate, primary considerations relate to system characteristics, research questions, data availability and social or policy concerns (Table 9; Figure 1). Although EWI metrics often require little *a priori* knowledge of systems, some system-specific information can help decide which or if EWI metrics are appropriate (Lade et al., 2013; Mantua, 2004). For instance, the presence of

hysteresis or thresholds may increase the cost of restoration, making detecting early warnings of regime shifts the more palatable option. Choosing when to use a metric will also depend on the research goal (e.g. active experimentation on regime shifts or passive monitoring) and data availability (sample sizes, is it spatial?, is it temporal?; Figure 1). In addition to ecological and statistical considerations, social or policy concerns can influence when or if to use EWI metrics. EWI metrics can provide evidence, and even estimates of confidence, to support the presence or absence of thresholds and regime shifts (Ives and Dakos, 2012; Rodionov, 2004). This can be used to inform policymakers and provide decision-making tools for managers. For example, an early warning signal could represent a policy “trigger point” for initiating management or restoration (Eason et al., 2016; Lindenmayer et al., 2013). The application of regime shift detection in rangelands is limited by data constraints (e.g., time-series and spatial data with sufficient resolution to cover relevant ecological scales are usually absent) and the lack of detailed knowledge for many traits, organisms and processes. However, several extant national or regional monitoring programs may provide data for testing the regime shift indicators reviewed in this paper. Several experimental monitoring initiatives (Nutrient Network, 2018; Borer et al. 2014) are underway to overcome this limitation.

Table 9. Questions and situational examples for determining when using regime shift/early warning indicator metrics (EWI metrics) could be appropriate. For each question/situation, the “Why” and “Why not” columns provide positive and negative support, respectively, for the use of EWI metrics.

Should I use Regime Shift or Early Warning Indicator metrics...	Why?	Why not?
<i>System Considerations</i>		
If hysteresis <i>is</i> present or likely?	- EWI metrics can allow management to prevent known or unknown imminent regime shifts. - Restoration of desirable states will be very costly or infeasible.	There is extensive knowledge of system drivers and hysteresis. Thus, applying finances, time, and effort to preventative management is more beneficial.
If hysteresis <i>is not</i> present or likely?	Restoration of desirable states, although possible or simple, will still be very costly.	- Same as above. - The cost to restore the desirable state is low.
<i>Research Question Considerations</i>		
While actively experimenting with thresholds or regime shifts?	- EWI metrics can quantitatively identify when/where thresholds or regime shifts occur. - Some EWI metrics can identify and rank relative influences of driving state variables (see Figure 1).	- Experimentation on thresholds could cause catastrophic or expensive consequences, so EWI metrics are not useful or advisable. - Early warning may not be necessary; simply identifying regime shifts (e.g., with proposed EWI or regime shift detection metrics) may be sufficient.

While passively monitoring state variables?	• EWI metrics can provide early warnings for unknown or unforeseen regime shifts. • EWI metrics can provide an estimate of the typical range of variability in a state.	• There are other statistical metrics or procedures in place.
To identify historic thresholds or regime shifts?	• Many EWI metrics have been used extensively to identify historic thresholds and regime shifts. • EWI metrics can provide quantitative and qualitative evidence of the present/absence of thresholds and regime shifts. • Some EWI metrics have explicit significance tests and can provide levels of confidence (see Figure 1).	• Early warning may not be necessary; simply identifying regime shifts (e.g., with proposed EWI or regime shift detection metrics) may be sufficient. • Some EWI metrics produce conflicting results when identifying historic regime shifts, so choosing the most appropriate metric can be challenging.
To detect spatial regimes?	• Some EWI metrics are amenable to detecting spatial regimes. • There is sufficient spatial data of the appropriate type to run EWI metrics amenable to detecting spatial regimes (see Figure 1).	• Data type requirements are not met for EWI metrics suitable for detecting spatial regimes.
At any spatiotemporal scale?	• Some EWI metrics are amenable to detecting spatial and temporal regimes. • There is sufficient spatial and temporal data of the appropriate type to run EWI metrics.	• Data type requirements are not met for EWI metrics suitable for detecting spatio-temporal regimes.
<i>Data Availability Considerations</i>		
If long-term temporal monitoring data is available?	• Many EWI metrics were designed and have been well-studied in temporal contexts. • Long-term temporal data can provide more accurate portrayals of the typical range of variability in a state. This in turn can increase the accuracy of EWI metrics. • Historic thresholds and regime shifts can be identified, providing insight into potential regime shift hazards in the future.	• There is extensive knowledge of system drivers and hysteresis. Thus, applying finances, time, and effort to preventative management is more beneficial.
If only spatial data is available?	• Some EWI metrics can use explicitly spatial data to detect early warnings of regime shifts (see Figure 1).	• Patterns may not be detectable with only one point in time.

	Some EWI metrics can use spatial data to identify spatial ecological regimes.	
If driving state variables are known?	- Some EWI metrics are designed for detecting thresholds or regime shifts with known driving state variables (see Figure 1). - Knowing driving state variables may increase the performance of EWI metrics and allow more accurate and earlier regime shift detection.	Monitoring known driving state variables may suffice for detecting imminent regime shifts and prioritizing management.
<i>Social or Policy Considerations</i>		
If social, policy, or legal concerns require confirmation of thresholds or regime shifts?	- EWI metrics can provide quantitative and qualitative evidence of the presence/absence of thresholds and regime shifts. - Policy or law mandates use of particular conceptual frameworks (e.g., state-transition models, ecological site descriptions) that would benefit from inclusion of quantitative metrics. - Some EWI metrics have explicit significance tests and can provide levels of confidence (see Figure 1).	- Available data are insufficient or not appropriate to detect early warning and regime shifts at the scale necessary to guide policy or to avoid misinterpretation and misuse. - There is extensive knowledge of system drivers and hysteresis, so applying finances, time, and effort for preventative management is less of a priority than focusing on sociopolitical constraints.

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Early warning metrics and regime shift detection provide practical tools to assess rangeland vulnerability and resilience in the face of rapid environmental change. Here, we draw upon three examples where the scientific exploration of these metrics can benefit core pursuits in the rangeland discipline. We encourage readers to read the full articles to obtain more information.

A

B

Time Step 0	Time Step 1	Time Step 2	Time Step 3
Smooth sumac (<i>Rhus glabra</i>) sparsely observed near center of selected grassland spatial regime, but no distinct sumac regime detected.	Simulated sumac island doubles in spatial extent, forms a closed canopy, herbaceous community under sumac shifts to shade-tolerant cool-season grasses, and dominant ground cover becomes leaf litter. Two emergent spatial regimes are detected (red = sumac regime; yellow = unknown regime).	Simulated sumac island again doubles in spatial extent with same patterns. Two emergent spatial regimes again detected (red = sumac regime; yellow = unknown regime).	Simulated sumac island again doubles in spatial extent. The former emergent regime (yellow) disappears, but now the northernmost spatial regime (black) becomes distinct from the southernmost regime (green).

Below the table in Panel B are four smaller aerial photographs corresponding to Time Steps 0, 1, 2, and 3, each with its own color-coded transect line showing the progression of the simulated sumac island and other spatial regimes.

Figure 29. The emergence of new states, and the potential to avoid collapses in existing states, has been a preeminent focus of rangeland ecology and management. Roberts et al. (in review) incorporate spatially-explicit application of a discontinuity analysis into field monitoring data collected along a 4 km transect at the Niobrara Valley Preserve, Nebraska, USA. This study identifies (A) the existing number and types of spatial regimes at the site, (B) the potential for using an early warning indicator in conjunction with the spatial regime concept to identify, via simulation of future field monitoring, the location and spatial scale at which a shrubland regime emerged, (C) and the expansion of the shrubland regime, at the cost to the previously dominant grassland regime, over time.

Example 2: Preparing management for system-level change: A fundamental problem in the development of leading indicators is that the performance of univariate indicators have been inconsistent, with high uncertainty surrounding their potential to predict future regime change (Brock and Carpenter 2012). Traditional (univariate) leading indicators also typically require the critical variables driving transitions to be known *a priori*, which is unrealistic in a future characterized by novelty and uncertainty. Spanbauer et al. (2014) and Sundstrom et al. (2017) assessed some of the multivariate indicators featured in this review and compared their utility to univariate indicators (Figure 30). These papers revealed a general problem all-too familiar to rangeland scientists and managers; that is, monitoring and management focused on a particular species or state variable of interest effectively masks community-level analyses from detecting system-level change. Both papers show that acting based on traditional univariate indicators becomes infeasible given the inconsistent signals and lack of spatial boundary detection needed to differentiate patterns among multiple populations of interest. In contrast, the authors concluded that more integrated measures that accommodate multivariate data have the potential to better reflect the reality of complex and adaptive ecological systems, like rangelands, and how to operationalize spatially-explicit signals of regime change.

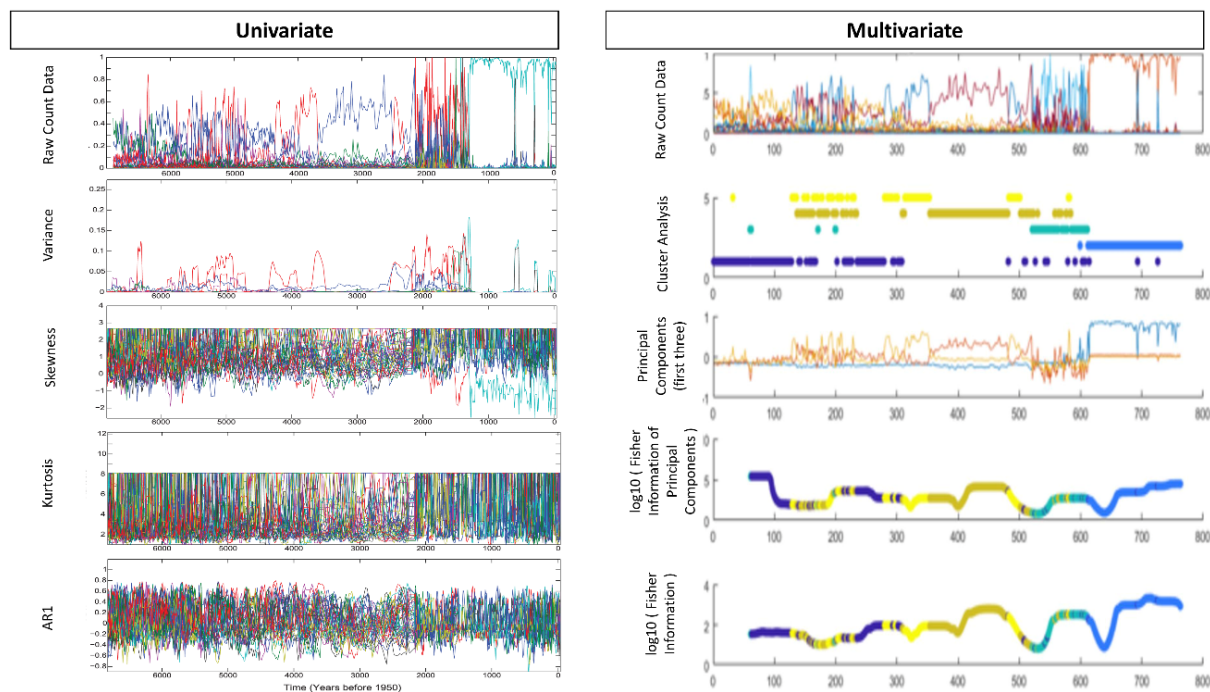


Figure 30. Integrative metrics that accommodate multivariate data are being explored to assess their potential utility to detect early warning and regime change in complex adaptive systems. Spanbaeur et al. (2014) compare various multivariate and univariate indicators using paleo-diatom data. Several populations of species experienced increased variability in this study, but conflicting patterns make it difficult to operationalize univariate statistics to characterize the behavior of this complex, multivariate system. Similar trends and observations might be expected in rangelands, but research has been limited, to date, to test these concepts and to assess their practical utility to rangeland managers.

Example 3: Advances in monitoring and application: Investments in technological innovation and computer processing is leading to rapid growth in strategic targeting tools that makes huge amounts of information and data readily accessible for rangeland science and planning. For example, utilizing robust ground level measurements, machine learning, and high performance cloud-based computing, Jones et al. (2018) produced annual maps with historical (1984-2017), continuous cover data (0 to 100%) of plant functional groups for US rangelands (Figure 31). The data product removed the barrier of single class, arbitrarily-delineated categorical data (e.g., where a pixel, landscape, or region is classified solely as grassland, shrubland, or tree), which removed information necessary to explore the potential utility of the early warning and regime shift metrics featured in this review. In addition, spatial risks or vulnerabilities to transitions can be identified and then management activities concentrated most effectively by utilizing frameworks that do not require or utilize *a priori* knowledge of states but instead focuses on transitions that are detectable and measurable. The coupling of these data and frameworks will prompt a shift from the static inventory and state mapping paradigm (Steele et al. 2012) within rangeland ecology to one of variability and transitions (Fuhlendorf and Engle 2001; Twidwell et al. 2013).

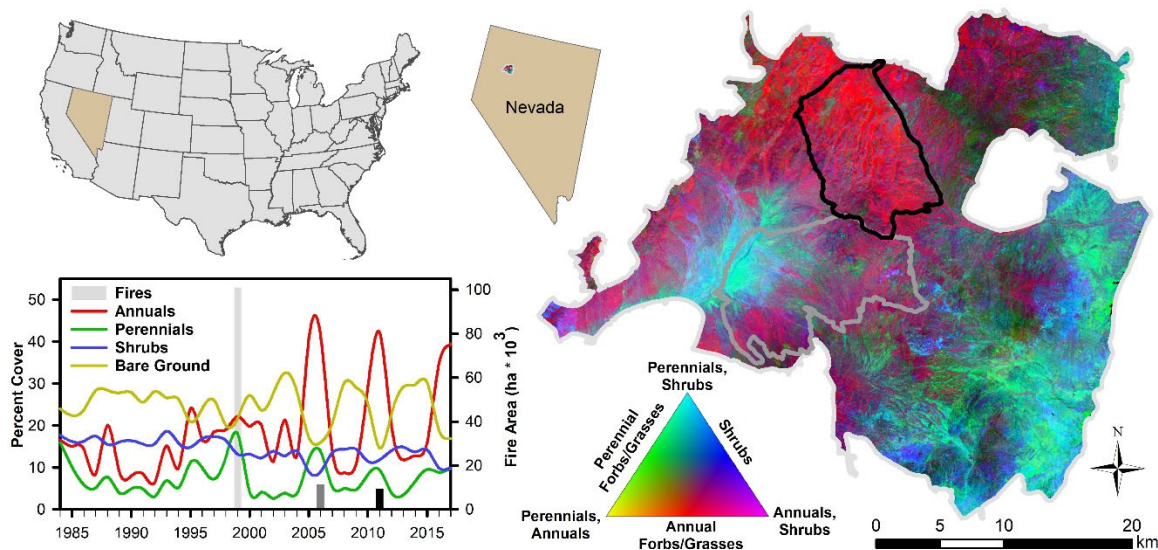


Figure 31. Future availability of remote sensing products with high spatiotemporal resolution has great potential to be incorporated into multivariate metrics used to detect early warning signals and regime shifts. Shown here are trends in annual percent cover of annual forbs/grasses, perennial forbs/grasses, shrubs, and bare ground from 1984-2017 within an area experiencing cheatgrass invasion. Bars denote the

area of the Dun Glenn fire and subsequent smaller scale fires that burned within the original fire perimeter.

Overall, the early warning/spatial regime paradigm represent quantitative, objective decision-making tools for rangeland management in the face of ecological uncertainty. Traditional inventory and monitoring efforts are not designed with the spatial specificity needed to provide indicators of sudden change in many rangeland systems; however, statistical theory is advancing to be able to better incorporate broad-scale monitoring and inventory data for purposes of early warning and regime shift detection. Moving forward, the quantitative metrics reviewed herein could fit into joint efforts to couple adaptive management and monitoring as part of a co-learning process – where the utility of the metrics are tested and the monitoring necessary for their application is critiqued while also using an iterative decision-making process to guide their adoption.

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APPENDIX A: List of Publications

- Allen, C. R., Angeler, D. G., Chaffin, B. C., Twidwell, D., Garmestani, A. (2019). Resilience Reconciled. *Nature Sustainability*: in press.
- Roberts, C. P., Twidwell, D., Angeler, D. G., & Allen, C. R. (2019). How do ecological resilience metrics relate to community stability and collapse?. *Ecological Indicators*, 107, 105552.
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