PERSONNEL

S.K. Morgan Ernest	PI	Utah State University	Dr. Ernest will be solely responsible for managing the proposed activities.

I. BACKGROUND

Dramatic changes in populations, communities, and ecosystems over short periods of time are a challenge for understanding ecological dynamics and have important implications for managing ecological systems. The need to detect, predict, and understand these changes, known as regime shifts has produced a growing body of conceptual and theoretical research (e.g. Scheffer et al. 2001, 2009; van Nes & Scheffer 2007). Regime shifts are defined as “abrupt changes in several trophic levels leading to rapid ecosystem reconfiguration between alternative states” and can be triggered by either nonlinear responses to small changes in ecosystem drivers (e.g. climate, nutrient input, biotic interactions) or by linear responses to rapid jumps in drivers (Fig 1; Andersen et al. 2009). Both types of regime shift can result in alternative states of the ecosystem that are difficult to reverse. Non-linear thresholds are inherently difficult to reverse (e.g. Scheffer et al. 2001) and if both linear and non-linear shifts are maintained for a long time, there are numerous ecological processes (e.g., priority effects, accumulated changes in soil nutrients) that make the return of an ecosystem to its previous state complicated or impossible (e.g. Ehrenfeld 2003; Fukami et al. 2010). Therefore, large and sustained changes in ecological drivers may generally send ecosystems into alternative configurations that are difficult to recover from.

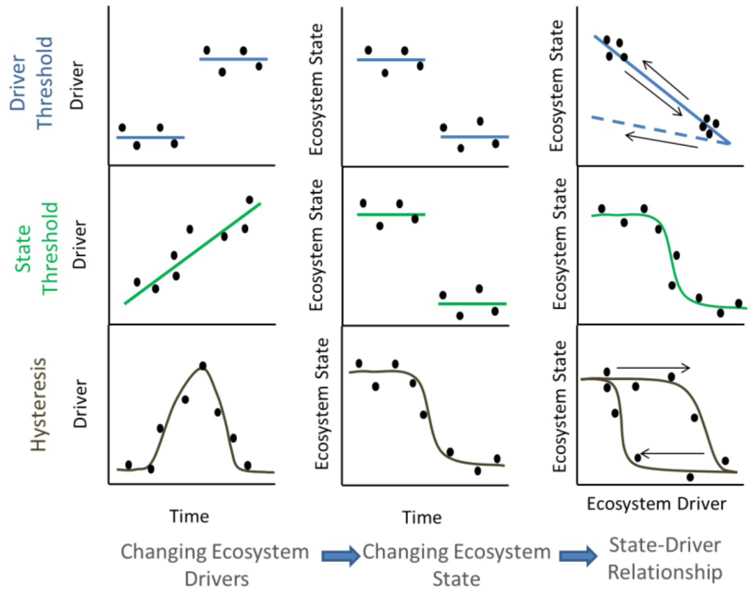

Fig 1. Three scenarios for regime shift involve jumps in drivers (top row), non-linear response of ecosystem state to drivers (middle), and different non-linear responses as driver increases & decreases (bottom). When a driver is reversed, ecosystem state may return to the initial state (solid line top right), return to initial state via an alternative pathway (bottom right), or exhibit a novel state-driver relationships (dashed line top right). Modified from Andersen et al 2009.

II. RATIONALE, OBJECTIVES & SIGNIFICANCE

Regime shifts represent a major concern for the management of ecosystems and the services they provide (Suding & Hobbs 2009). It is critical to understand how they occur, what form the transitions take, and if they are reversible. While substantial progress has been made in the theoretical understanding of regime shifts, empirical evaluation has lagged behind due to the inherent challenge of studying rapid transitions. Current research is focused on assessing shifts in ecosystem time-series to determine if the changes in ecosystem state are different from the background state of the system and whether the dynamics correspond to changes in suspected abiotic or biotic drivers (deYoung et al. 2008; Andersen et al. 2009). Unreplicated observational studies are inherently limited with respect to identifying underlying mechanisms (Schröder et al. 2005; deYoung et al. 2008), and they do not allow evaluation of one of the most critical aspects of regime shifts – reversibility. Replicated experiments, where a regime shift is experimentally induced would allow for more rigorous assessment of how ecosystems respond to regime shifts (Boettiger & Hastings 2012). **I will reverse an existing set of long-term manipulations to rigorously assess conceptual models of regime shift, whether or not these shifts are reversible, the impact of the magnitude of the driver shift on ecosystem dynamics, and how these shifts differ among different components of the ecosystem.**

The most difficult issues of regime shifts to assess are if shifts are reversible and whether return to the initial state occurs along the same or different pathways (Fig 1, bottom right; i.e., hysteresis). The reversibility of regime shifts is difficult to assess because ecosystems are likely to have more than one driver that is changing (e.g., climate, nutrients, fragmentation, extinctions). Once a driver is restored, it becomes difficult to know if an ecosystem fails to converge to a 'previous ecosystem state' because an alternative ecosystem state was created by the driver change or because changes in other drivers shifted the state of the system. This issue also impacts our ability to assess hysteresis. Unless the driver is manipulated in both directions under the same conditions, differences in ecosystem reassembly could be due to differences in the states of other drivers. Ideally, a regime shift experiment includes replicates experiencing differences in driver state where the driver state could be flipped simultaneously in a subset of those replicates. This design allows replicate plots experiencing driver shifts to be compared to reference plots that would exhibit the 'target state' for that specific driver condition given the current environment (Fig 2). Only with this type of design is it possible to rigorously assess the reversibility of regime shifts under field conditions.

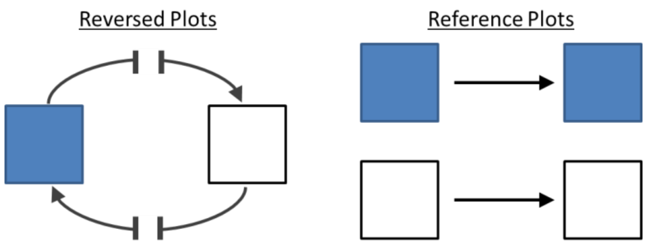

Fig 2. Reference & Reversed Plots Concept. The design consists of plots in two driver states (white & blue). For some plots driver state is disrupted, flipping the ecosystem (reversed plots) but maintained in other plots (reference plots)

While this design is ideal, it is not typically used because it is difficult to implement. Conducting replicated experiments at a scale where alternative states can be generated is challenging, which explains why few regime shift studies involve replicated experiments and fewer still occur under field conditions (Schröder et al. 2005). Even more challenging is the fact that the two manipulations need to actually switch between states, not simply directions of the manipulation, which requires that alternative states already be established before the simultaneous reversal can occur. Finally, the ecosystem driver must be easily manipulated. While few field systems fit all of these criteria, those that do will be critical for rigorously assessing theoretical and conceptual aspects of the regime shift concept.

I will use an existing long-term experiment where a sustained but easily reversed manipulation of the rodent community has generated strong differences in plants, animals and soil nutrients (see further discussion below). I propose to reverse the manipulations on a subset of existing control and manipulation plots to monitor how these replicated plots respond to a rapid transition in an important biotic driver. I will use this experimental system to ask four critical questions: **1) When ecosystem drivers jump to a new state, how do ecosystems reorganize? 2) Are these changes reversible? 3) How does the magnitude of the driver shift influence the reversibility of a regime shift? 4) Do different components of an ecosystem transition in concert or exhibit idiosyncratic responses to driver shifts?**

III. EXPERIMENTAL PLAN

STUDY SITE: I will use an existing long-term experiment near Portal, AZ. For the past 35 years rodents have been manipulated to study the impacts of competition and granivory on a Chihuahuan Desert ecosystem. The site consists of 24 permanent plots, each 0.25 ha in size, surrounded by a hardware cloth fence. Plots are assigned to one of three treatments: 1) Control plots have 16 large holes cut in the plot fencing permitting free access to all rodents; 2) Kangaroo rat removals have smaller holes preventing access to the large-skulled kangaroo rats; and 3) Rodent removal plots do not have holes and any rodents that are caught on the plots are removed. Additional manipulations have been performed on some plots in the past, but none had a substantial influence on the system so these manipulations were stopped (Brown 1998). From 1977-1987, 8 plots had seeds added or plants removed but there was little effect on rodents, plants, or ants and these plots were reassigned to rodent manipulations in 1988. Ants were also manipulated on a subset of plots, but these treatments had only weak effects on plant composition (Guo & Brown 1996) and no impacts on rodents (Samson et al. 1992), so ant manipulations ended in 2009.

EXISTING MANIPULATIONS & ALTERNATIVE STATES: The experimental manipulation of rodents has been maintained for decades and created plots that exhibit major differences in plant composition (e.g. Supp et al. 2012), soil nutrients (Baez 2007; Smith et al in prep), plant species richness and abundance (Supp et al. 2012), shrub establishment (Valone & Thornhill 2001), and response to invasive species (Allington et al. 2013). In addition, removal of a single genus of rodent (kangaroo rats) has created plots that differ from controls in rodent resource consumption (Thibault et al. 2010a), response to colonizing species (Ernest & Brown 2001) and rodent responses to precipitation events (Thibault et al. 2010b). These sustained responses of population, community, and ecosystem level properties, to an easily reversible manipulation provide an ideal context for experimentally studying regime shifts in a natural system.

EXPERIMENTAL REGIME SHIFT & MONITORING: I will reverse experimental manipulations on12 of the 24 plots at the study site: 3 controls converted to rodent removals, 3 rodent removals converted to controls, 3 kangaroo rat removals converted to controls, and 3 controls converted to kangaroo rat removals. The remaining plots will maintain their existing manipulation (4 controls, 3 rodent removals, 5 kangaroo rat removals). We will maintain the long-term data collection on winter and summer annual plants (16- 0.25 m^2 quadrats/plot sampled twice annually), ants (annual colony counts conducted at 49 permanent stakes/plot), and rodents (monthly trapping at 49 permanent stakes/plot) on all plots. In addition to continuing existing data collection activities, I will increase the resolution of the time series by sampling ants monthly when ants are active and implement monthly sampling of soil nutrients by collecting 10 soil samples from each plot (half under shrub cover and half in the open; Schlesinger & Pilmanis 1998). Soil samples will be processed by the USU Analytical Lab. Total nitrogen and soil organic carbon will be analyzed because previous studies showed differences between controls and manipulations (Baez 2007; Smith et al. in prep). Baseline data will be collected before manipulations are reversed. Plots will be monitored for 5 years to assess responses to manipulation reversals.

IV. RESEARCH QUESTIONS

Aim 1: When ecosystem drivers shift rapidly, how do ecosystems reorganize? I will evaluate 4 alternative hypotheses: 1) the ecosystem responds immediately to the change by jumping to a new state (Fig 1 top center); 2) the ecosystem responds immediately, but gradually, to a new state over a relatively long period of time; 3) the ecosystem does not respond even though the change in state has caused the system to change states in the past; and 4) the system does not change initially and then exhibits either a linear or non-linear shift to a new state. The general form of the response will be assessed using generalized additive modeling (Hastie & Tibshirani 1990).

Aim 2: Are observed changes reversible? I will evaluate 3 alternative hypotheses: 1) ecosystem state changes along the same pathway regardless of the direction of driver change (Fig 1 top right bold line); 2) driver direction impacts ecosystem reorganization, but systems eventually converge to a single state (Fig 1, bottom right); and 3) accumulated changes caused by long-term driver change prevent ecosystems from returning to their original state (Fig 1, top right dashed). Simultaneous reversals of controls to manipulations and vice versa allows rigorous assessment of whether transitioning a driver between two conditions results in ecosystems reorganizing along the same trajectory or along different trajectories because it controls for changes in other drivers (e.g. climate). For multivariate responses such as species composition, canonical analysis of principal components (CAP) will be used to test the hypotheses that the species composition of reversed controls and reversed rodent removals become more similar through time and whether they diverge or converge from maintained controls and rodent removals (Anderson & Willis 2003). For univariate responses such as total nitrogen, a mixed model (e.g. GLM) will be used to assess differences among groups.

Aim 3: How does the magnitude of the driver shift influence reversibility? There are two alternative regime shift hypotheses for how ecosystems respond to different degrees of change in the same ecosystem driver: 1) if regime change is non-linear (Fig 1 center right) then if a change in ecosystem state occurs then the magnitude of that change and its reversibility will be independent of the magnitude of the change in the environmental driver, because any change in driver sufficient to cross the threshold will result in a rapid, non-linear shift (Scheffer et al. 2001); 2) if regime change is linear (Figure 1 top right) then shifts caused by small changes in the driver will be smaller and more reversible because the distance from the initial state is smaller and there is no threshold to overcome (Scheffer et al. 2001). Because rodent and kangaroo rat removals represent different magnitudes of the same driver change, and this driver change is sufficient to induce changes in the ecosystem, the experimental design provides a unique opportunity to compare recovery from a large driver shift (return of the full rodent community to plots) with a smaller driver shift (return of kangaroo rats to the rodent community). I will compare dynamics between the kangaroo rat and rodent removals to assess whether the degree of driver shift alters how ecosystems reorganize. I will assess whether there are differences between reversed kangaroo rat and rodent removals in whether they return to the reference state and the rate at which they do so by comparing the distance (e.g., multi-dimensional scaling [MDS; Cox & Cox 2001] for multivariate responses like species composition) between the reversed and relevant reference plots as a function of time.

Aim 4: Do different components of an ecosystem exhibit different responses to driver shifts? How different components of an ecosystem respond to drivers is poorly understood. I will evaluate whether plants, ants, mammals, and nutrients respond differently to shifts in drivers and if so whether differences are related the life history of the organisms and the dynamics of the abiotic processes involved (deYoung et al. 2008). Because of lifespan differences, presence of resistant stages, and dependence on changes in other ecosystem processes (soil nutrients are influenced by both rodents and plants), I predict a distinct order of ecosystem response (from quickest to most lagged): rodents, annual plants, ants, and nutrients. For each component, the distance (i.e., MDS for multivariate responses) between reversed and relevant reference plot will be calculated for each year. This measures the magnitude of the response, controlling for the reference state, and allows comparison of the magnitude of the response as a function of time since manipulation. If different components of the ecosystem differ in their response time to a regime shift, as seems likely, then focusing monitoring efforts on rapid response groups may prove an important early warning signal that a regime shift has begun. Regardless, understanding how multiple components of an ecosystem are responding in concert to a regime shift is a critical step in regime shift research.

V. BROADER IMPACTS

Several broader impacts will be supported by this project. 1) *Data publication*: Data from 1977-2002 is already published on Ecological Archives (Ernest et al. 2009). This proposal will support publishing the next 10 years of data (2003-2013). All data collected for this proposal will be made available on-line 1 year after its collection. 2) *Data use*: The complicated structure of the long-term data hampers its accessibility and use. To increase data use, we will write software in the 3 most widely used languages in ecology: SQL, R, and Python. These programs will generate easily extracted summarized data. Programs will be posted on GitHub (https://github.com/weecology) and advertised broadly. 3) *Recruiting:* Graduate students, a postdoc, and undergraduates will be supported on this project. Recruitment for undergraduate and graduate student positions will involve targeted outreach to undergraduate biology mentoring programs at southwestern universities where minority enrollment is > 20%. 4) *Training:* Because regime shift research is highly theoretical and computational, students will be trained in computational ecology using existing courses at USU. Funds will be allocated each year to send trainees to workshops on topics related to modeling, database management and programming and to host workshops at USU taught by Software Carpentry (software-carpentry.org), an international group whose mission is to teach good computational practice to scientists. 5) *Outreach*: Understanding how regime shifts occur and their reversibility are a management concern (Suding & Hobbs 2009). Results from this project will be reported to land management agencies (e.g., Arizona Fish & Game, Bureau of Land Management).