MECHANISTIC FOUNDATIONS OF STATE AND TRANSITION MODELS: LINKING APPLICATION AND THEORY

INTRODUCTION

Rangeland systems, particularly those in arid and semiarid regions, exhibit complex dynamics in response to disturbance (i.e., grazing) and climate variation (i.e., drought). Substantial shifts in vegetation can occur with little forewarning and once the shifts occur they may be difficult to reverse (Schlesinger et al. 1990, Gunderson 2000, Scheffer et al. 2001, Foley et al. 2003). Incorporating this complexity in the development and evaluation of management frameworks has been a long-standing challenge (Allen-Diaz and Bartolome 1998, Fernandez-Gimenez and Allen-Diaz 1999, Briske et al. 2003, Stringham et al. 2003).

Rangeland ecology has operationalized the inclusion of complex dynamics through the development of state and transition models. State and transition models of rangeland vegetation dynamics split changes in rangeland ecosystems into discrete states and describe processes that cause transitions between states (Westoby et al. 1989, Friedel 1991, Briske et al. 2003). This framework was proposed in the late 1980's (Westoby et al. 1989) and is currently regarded as a robust and accessible method for qualitatively describing ecosystem dynamics in a decision-making context for managers of rangeland systems (but see Cowling 2000, Oba et al. 2000). However, these models have tended to be phenomenological rather than mechanistic and, as a consequence, their utility for making predictions is limited.

Over ten years ago the National Research Council recommended that "…*USDA should initiate a coordinated research effort … to develop, test, and implement new models of rangeland change that incorporate the potential for difficult-to-reverse shifts across ecological thresholds*" (NRC 1994). Descriptions of rangeland states are expanding through the use of state and transition frameworks and the development of the Ecological Site Description Database, a program for ecological site description information through the Natural Resource Conservation Service of the USDA (http://esis.sc.egov.usda.gov/). However, determining the complex interactions that make some rangelands at risk has yet to reach fruition. **A parallel approach – tests using experimental manipulations of the indicated critical transitions – can enhance the efficacy of such descriptive knowledge bases.**

We propose to test the generalities and predictability of grazing intensity, widely thought to drive transitions between rangeland states, and its impact on ecosystem processes. In addition, we will investigate how vegetation change initiated by grazing intensity may promote positive plant-soil feedbacks involving microbes and important limiting resources such as water and nitrogen, increasing the resilience of rangeland vegetation states. We focus on ecosystem states of management concern in California rangelands: perennial native grasslands dominated by species such as Needlegrass (*Nassella pulchra*), annual exotic grassland state dominated by acceptable forage species such as soft chess (*Bromus hordeaceus*) and wild oats (*Avena fatua*), and annual exotic grassland dominated by noxious weeds such as Medusahead (*Taeniatherum caput-medusae*). In our research, we ask two questions:

(1) Does grazing intensity drive rangeland systems to **cross state thresholds**, thus precipitating sudden changes in species composition and ecosystem functioning?
(2) Are there underlying **positive feedback** mechanisms that promote the resilience of less desirable rangeland states and affect transitions to states that are more sustainable?

We will investigate ecological processes that lead to the restoration and retention of efficient and sustainable functioning in rangeland ecosystems. **By pushing these systems experimentally, we can determine factors that influence ecological thresholds and resilience.** With this approach, we will identify factors that may facilitate or impede the conversion or restoration of degraded rangeland systems to more sustainable ones. By quantifying how ecosystem processes interact with vegetation and possible drivers of vegetation change, **we link these tests with the investigation of the smaller-scale feedback mechanisms that may cause the larger-scale threshold dynamics.** By perturbing both sustainable and degraded rangeland, we will be better able to **identify rangeland systems *at risk* of shifting** across difficult-to-reverse ecological thresholds ***before they actually collapse***.

In the following section, we review rangeland models and the evidence supporting state and transition models in California rangeland. Then, in section II, we describe how theory can be integrated with empirical tests. In sections III and IV, we detail our hypotheses and experimental approach. We end with specifics of project management and a timetable (section V), and a summary of the significance and implications of this proposed research (section VI).

I. RANGELAND MODELS AND EVIDENCE FROM CALIFORNIA RANGELANDS.

Climax-succession-retrogression models, also termed Range condition models (Allen-Diaz and Bartolome 1998), historically provided the context for range management (Dyksterhuis 1949). In this framework, systems are assumed to return to their pre-disturbance state or trajectory following abiotic disturbance or intense management (e.g., overgrazing). This theory predicts a classical successional trajectory: steady, directional change in composition to a single equilibrium point (Clements 1916, Odum 1969). In this framework, the removal or reduction of livestock use or other degrading factors should return California grasslands to original perennial grass dominance (Heady 1958). These models predict tightly coupled relationships between herbivory and the production and composition of rangelands and little threshold behavior.

In the late 1980's, the possible existence of multiple stable states was recognized in *state and transition models*, which were suggested as an improved framework for semiarid and arid rangeland systems (Westoby et al. 1989, Friedel 1991). These models describe persisting "states" characterized by different vegetation composition and definable "transitions" between states (Westoby et al. 1989). Transitions are often described as triggered by extrinsic events (climate, fire, etc.), management actions (seeding, changing stocking rate, etc), or a combination of the two. The basic premise behind these models is that overgrazed rangelands often do not recover when grazing pressure is reduced. For instance, grassland recovery in many shrub-invaded sites in the southwestern US is limited by changes in fire frequency and the spatial distribution of soil resources caused by the shrubs (Schlesinger et al. 1990, Van Auken 2000), resulting in a persistent shrub-dominated ecosystem even after overgrazing stops. These models recognize that unstable equilibria and discontinuous transitions are important to describe vegetation dynamics in rangeland systems. They represent one of the best cases where complex dynamics have been applied to management of ecosystems.

State and transition models are well developed for many rangeland systems and can be used by managers as a guide to apply understanding of these ecosystems (USDA 1997, Bestelmeyer et al. 2003, Stringham et al. 2003). They are excellent communication tools to discuss the dynamics of the site with a land manager and assist land managers in making timely, well-informed management decisions. While this approach is generally well-accepted and an excellent framework to manage rangelands, there have been few quantitative tests (Iglesias and Kothmann 1997, Bestelmeyer et al. 2003, Briske et al. 2003, Stringham et al. 2003). Current use of these models is largely conceptual and descriptive (e.g., see Fig. 1). In contrast, recent advances in complex dynamics have been largely theoretical. Although experimental evidence generally supports the relevance of multiple stable states in ecological systems (Schroder et al. 2005), empirical tests that can join the two approaches are increasing but lag far behind (Sterner and Elser 2002, Foley et al. 2003)

<u>California Rangelands</u>. State and transition models have been well-developed in rangelands of California (George et al. 1992, Jackson and Bartolome 2002). Continuous high-intensity livestock grazing began in the mid nineteenth century and is believed to have contributed to these grasslands being increasingly dominated by exotic species from other Mediterranean regions (Heady 1977). It is estimated that 9.2 million hectares of California rangelands are now dominated by exotic species (Jackson 1985), a highly persistent rangeland state that can dramatically change ecosystem processes (Christian and Wilson 1999). Currently native perennial grasslands account for less than 1% of their estimated range prior to 1800 (Freudenberger et al. 1987). Exotic annual species have maintained dominance in many areas where grazing has ceased for over 30 years but stands of native grasses persist under many historical levels of grazing (Stromberg and Griffin 1996), patterns consistent with a state and transition model.

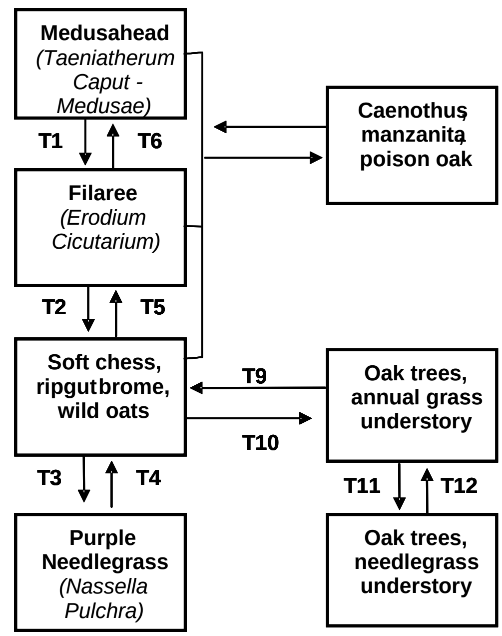

Figure 1 State and transition model for a foothill rangeland in Yuba County, California (after George et al. 1992). The dominant species of each state are listed above. Transitions between states are denoted by numbers, for example **T1**: Seemingly irreversible, but Medusahead seedbank may be reduced by several forms of disturbance (e.g., herbicide, cultivation, late May fire). **T3:**. Heavy early spring grazing followed by late summer burning and adequate rest between grazing periods may facilitate this transitions. **T4**: Year-long continuous grazing, drought, competition. These transitions are generally based on observation and experience, and rarely are accompanied by explicit experimental tests.

To test the applicability of state and transition ideas, we focus on previously identified states and transitions in California rangelands. In particular, we focus on the series of grass-dominated states identified by George et al. (Fig. 1, 1992): exotic noxious annuals (e.g., Medusahead, *Taeniatherum caput-medusae*) to acceptable forage annuals (e.g., soft chess, *Bromus hordeaceus* and wild oats, *Avena fatua)* to native perennials (e.g., Needlegrass, *Nassella pulchra*). Grazing, water, and nitrogen are all implicated to play possible mechanistic roles in the transitions between these grass-dominated states. George and co-workers also listed a Filaree dominant state but the transitions between it and alternative grass states suggest that it may be a transient and unstable state; for simplicity we omit it in our current treatment. (Note here that we use the term "state" in the context of state and transition models: they have not been tested to determine whether they meet the criteria of multiple stable states.)

California rangelands are an excellent model system for the study of states and transitions in management because the seemingly most resistant state is dominated by a noxious weed (Medusahead), while the native perennial (*Nassella pulchra*) is a desired native perennial forage species. The intermediate state, dominated by the exotic annual grasses soft chess (*Bromus hordeaceus)* and wild oats (*Avena fatua)*, is also preferable forage compared to Medusahead. Thus, there is strong practical motivation to understand the mechanisms that can lead to persistent dominance of Medusahead as well as the factors determining the potential for restoration to native grassland. All three states exist at our study site and are correlated with grazing history.

Several general lines of evidence suggest that grazing plays a major role in mediating the interactions between these California grassland species. Plant species in general, and native perennial and exotic annual grasses in particular, are expected to experience a tradeoff in their abilities to compete for resources and their abilities to tolerate grazing (Busso et al. 2001, Hendon and Briske 2002). Intense grazing could reduce the competitive ability of perennial grasses more than that of annual grasses, effectively switching the dominance hierarchy. Perennial grasses would be superior soil resource competitors under low intensity grazing conditions but poorer competitors under high intensity grazing (Grover 1997, Diaz et al. 2001). Our results from a four-year mowing experiment support this prediction (Harpole, unpublished results, Fig. 2, 3).

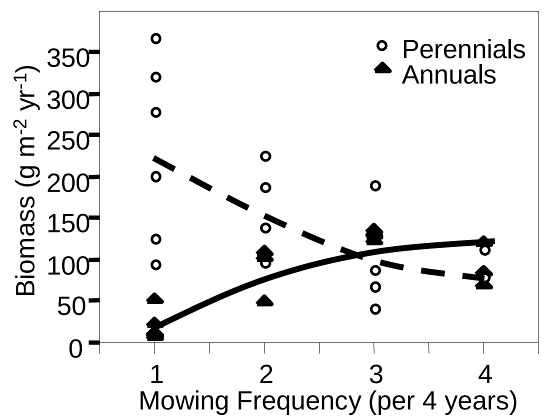

Figure 2. Exotic annuals increase (solid line) and native perennials (dashed line) decrease with increased mowing frequency. Mowing and grazing have been shown to have similar effects in these systems, and so we expect to see a similar relationship with grazing intensity.

The existence of these different rangeland states also has large implications for sustainable ecosystem management (Christian and Wilson 1999). Areas invaded by exotic annual grasses have higher rooting profiles, higher soil moisture at deep levels, higher soil nitrate concentrations, and lower early-season light levels relative to areas with native perennial grasses (Joffre et al. 1987, Dyer and Rice 1999, Seabloom et al. 2003a). Consequently, exotic annual rangelands have increased microbial activity, lower soil carbon storage and less capacity to retain nitrate (Eviner and Chapin 2002, Eviner 2004) (Fig. 4). These differences in root allocation and soil carbon also lead to increased risk of erosion and soil instability (Jackson et al. 2000). Thus, changes in vegetation states driven by grazing also have the potential to set up self-reinforcing feedback cycles (Wilson and Agnew 1992).

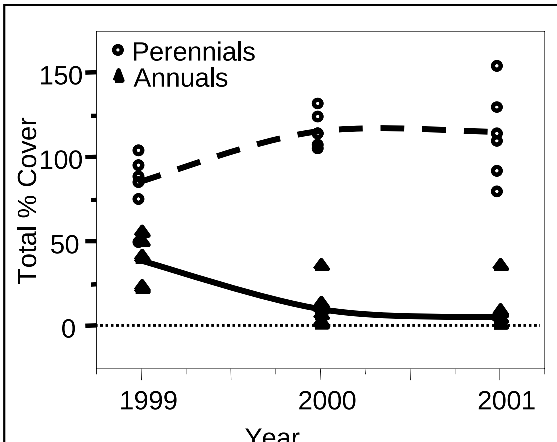

Figure 3. In ungrazed areas, perennial native grasses (dashed line) are able to maintain dominance and exclude exotic annual grasses (solid line). Recruitment limitation was overcome by adding seeds of the native species, a technique we will use in the proposed work.

One such feedback mechanism that might contribute to resilience of rangeland states is through nutrient cycling. There is evidence that both native perennial grasses and exotic annual forage grasses (less work has been done on Medusahead) impact soil resources in a way that may increase their success. For instance, native perennial grasses can reduce soil moisture to lower levels than do exotic annual grasses, decrease nitrogen levels during times of the year when water is limiting, and can sustain growth at lower levels of nitrogen than annuals (Seabloom et al. 2003b). In contrast, exotic annuals use soil moisture less completely, which should promote microbial activity and nutrient cycling and consequently the high nutrient conditions which have been shown to promote their dominance (Harpole, unpublished data). In addition they produce litter that is fast to decompose, enhancing N-mineralization by microbes, increasing plant available N (Wedin and Tilman 1993). Annual grass species with low tissue C:N might thus foster high-N conditions under which they are better competitors for another resource like light, whereas native perennial grasses might foster low-N conditions under which they are better competitors (Wedin and Tilman 1993, Craine et al. 2002, Suding et al. 2004b).

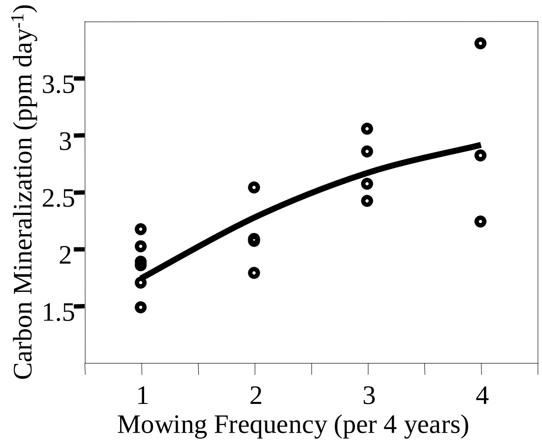

Figure 4. Accompanying an increase in exotic annual grasses, microbial activity and carbon mineralization increases with increased mowing frequency. These areas also have lower carbon storage and less capacity to retain nitrate.

Feedbacks between the soil microbe community and plants can also reinforce vegetation states in rangelands. Plant species can "culture" different suites of soil microorganisms with the consequence that each species grows better in its own soil and worse in the other's soil (Bever 2003). Recent work by K. Vogelsang and J. Bever (2003) in Southern California demonstrated soil community changes in annual exotic grasses generated by the specificity of response in plant-microbe interactions between native and annual grasses. These effects can occur through interactions with mycorrhizae as well as pathogens in the soil (Klironomos 2002). While these effects can be negative or positive, in the case of the work in California rangelands (Vogelsang and Bever 2003, as well as Grman and Suding, unpublished results), these effects have been shown to increase the success of the modifying species.

II. INTEGRATING THEORY AND EMPIRICAL TESTS

State and transition models in semiarid rangelands are designed to conceptually describe *multiple state equilibrium dynamics* (Bestelmeyer et al. 2003, Briske et al. 2003, Stringham et al. 2003). These models describe cases where a system can achieve different but mutually exclusive resting or locally stable states, any of which are possible but entirely dependent on the initial conditions of the system (see reviews by Scheffer et al. 2001, Beisner et al. 2003). Between these locally stable states are unstable regions from which positive feedbacks drive the system towards one or another stable point (Fig. 5). Each stable state is relatively resistant to change but if forced past some threshold into the unstable region, it can rapidly shift to another state. Dramatic shifts in systems can occur when slowly-changing external drivers cross threshold transitions (Rietkerk and vandeKoppel 1997, Augustine et al. 1998, Scheffer et al. 2001, van de Koppel et al. 2001, Augustine et al. 2003).

While the ideas surrounding resilience, thresholds, and multiple stable states are appealing in their application to semiarid rangelands, very few empirical tests exist. Recent developments linking theory and application related to complex dynamics can advance the way we develop and test management strategies for rangeland sustainability. Increasingly, there is a consensus on a group of empirical tests that are stringent yet feasible enough to test the theory (Scheffer and Carpenter 2003, Schroder et al. 2005). **We use the following four tests as the basis for our experimental approach and hypotheses:**

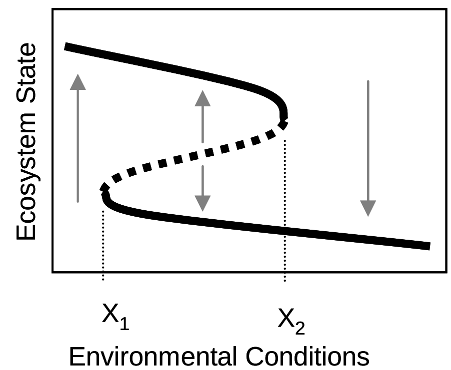

Figure 5. Although systems can respond smoothly to a change in external conditions, they can also sometimes change profoundly when conditions reach a critical level. *Multiple Stable States* describe the case (above) where a system can have more than one state over a range of conditions (i.e., between X_1 and X_2). Only one state occurs below X_1 and above X_2 in this example. The dotted line indicates a region of unstable equilibrium.

1. **Non-recovery after perturbation**. If the perturbation that drove a change in state is removed, the system does not revert to its original state. This is the basic premise behind state-and-transition models: overgrazed rangelands often do not recover when grazing pressure is reduced.
2. **Divergence of the system from different initial conditions**. Starting the system with different species composition (or different density ratios) should lead to alternative final states (Chase 2003, Scheffer and Carpenter 2003). A corollary is that these states are not invasible by the other state once they are established.
3. **The system will exhibit hysteresis**. An ecosystem shift in response to a small environmental change will not be reversible by an equally small environmental change in the other direction. Such hysteretic responses have obvious importance for managing or restoring ecosystems (Scheffer et al. 2001, Suding et al. 2004a).
4. **The presence of positive feedbacks**. Positive feedbacks amplify small deviations and either push a state into a different region of attraction or allow it to return to its original state. Negative feedbacks then stabilize the system locally, establishing stable states.

We will use this series of tests to ask whether rangelands in California follow dynamics predicted by state-and-transition models. This approach is powerful and innovative in that it will A) **experimentally test the generality and predictability of processes** thought to drive transitions; B) test whether several **smaller-scale feedback mechanisms** contribute to threshold dynamics; and C) use **experimental results to parameterize mathematical models** in order to extend our predictive ability. We propose to apply mathematical consumer-resource models (Tilman 1982, Grover 1997, Chase and Leibold 2003) to these questions because of their mechanistic basis and their ability to be directly parameterized from and tested with experimental field data. This type of model allows explicit modeling of ecosystem processes of interest such as resource use, carbon storage, and productivity and forage quality (e.g., tissue C:N) (Grover 1997, Chase and Leibold 2003) and can be extended to include positive feedback effects. As a whole, the project will serve as a test of how multiple types of dynamics can be empirically investigated and incorporated in predictive frameworks of sustainable land management.

III. HYPOTHESES.

Our hypotheses are based on three ecosystem states of management concern in California rangelands: perennial native grasslands (dominated by species such as *Nassella pulchra*), annual exotic grassland state dominated by acceptable forage species such as soft chess (*Bromus hordeaceus*) and wild oats (*Avena fatua*), and annual exotic grassland dominated by noxious weeds such as Medusahead (*Taeniatherum caput-medusae*) (Fig. 6). Based on criteria to demonstrate multiple stable state dynamics (outlined in section II), we test the following hypotheses. These hypotheses are not presented as alternatives but rather as a series of parallel tests that, if supported, would provide multiple lines of evidence favoring state-and-transition models. Alternatively, lack of support for these hypotheses would suggest that rangeland dyanamics are largely continuous and gradual in nature, supporting classical range condition models.

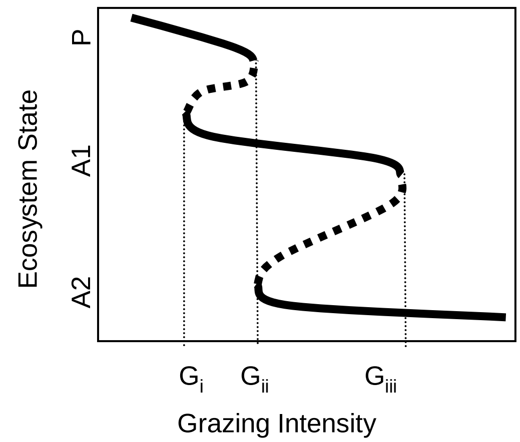

Figure 6. Predicted rangeland states and their sensitivity to grazing intensity based on state and transition models. P=perennial native grasses, A1=acceptable annual exotic grasses, A2=noxious annual grasses (Medusahead). G_i-G_{iii} are levels of grazing intensity where transitions among states should occur.

H1: ***Undesired rangeland states will persist after the cessation of grazing.*** In our study system, Medusahead dominates heavily grazed pastures (A2 in Fig. 6). In these pastures, we predict that a reduction in grazing intensity will not result in a gradual change towards increased abundance of acceptable forage annuals (A1 in Fig. 6). Instead, Medusahead will maintain dominance as grazing pressure is reduced. Because seed limitation may give the appearance of non-recovery (Seabloom et al. 2003a), we will add seeds of all species in our experimental treatments. Likewise, we expect to see similar dynamics in areas of intermediate grazing intensities that are dominated by acceptable forage annual species: reducing grazing pressure further in the presence of native perennial propagules will not result in a gradual change towards the increased abundance of native perennials.

Test of H1 (non-recovery). To test this first hypothesis, we will manipulate grazing pressure in heavily-grazed pastures dominated by Medusahead (A2) and in moderately-grazed pastures dominated by acceptable forage annual species (e.g., *Bromus* and *Avena*) (A1). In all manipulations, we will add the propagules of our three focal groups: noxious annuals, acceptable forage annuals, and native perennial grasses. If the hypothesis is supported, we expect to find that the original dominant in the pastures (Medusahead in heavy grazed and Brome in moderately grazed) will be relatively resistant to the invasion of the other groups, and able to persist across a range of grazing intensities. We will not conduct parallel tests in native perennial grasslands to avoid damaging these systems by introducing exotic species.

H2: ***Multiple rangeland states can persist under similar grazing regimes.*** Under certain grazing regimes, multiple types of rangeland can persist, depending on initial conditions and priority effects. We expect that multiple stable states consisting of either dominance of Medusahead or Brome species will occur at moderately high grazing intensities. Similarly, we expect that multiple stable states consisting of either Brome or native perennial grass dominance will occur at low grazing intensities. We will use the reciprocal invasion criterion (Chase and Leibold 2003) to test these predictions: 1) each species group must be able to maintain a population when grown alone, and 2) each species group must be unable to invade established populations of the other groups.

We also predict that at extreme grazing intensities (i.e. below G_i and above G_{iii} in Fig. 6), no alternative states will exist. Ungrazed and highly grazed rangelands should converge to native perennial grass and Medusahead dominance, respectively. These states should be relatively uninvasible by the other grassland groups.

Tests of H2 (divergence). To test our second hypothesis, we will remove priority effects with a solarization treatment in each of the pasture types. Solarization involves tilling and then covering the soil with plastic for a period of time, thus trapping solar heat to reduce effects of the prior species such as seed bank or microbes (EPA 1996). After solarization, we will establish populations of each of the three species groups at all sites. We predict that each should be able to establish in all pastures, indicating weak environmental control on dominance patterns and meeting the first criterion of the reciprocal invasion test (see above).

After establishment, the populations will be exposed to a gradient of grazing intensities. We will reciprocally "invade" species into each established population through a series of seed additions. At high grazing intensities (above G_{iii} in Fig. 6) we predict that only Medusahead populations will persist and that Medusahead will be able to invade and dominate the other populations. As grazing intensities are reduced, we expect to see conditions where both Medusahead and Brome can persist and both can invade native perennial grass populations, but neither can successfully invade the other (i.e., between G_{ii} and G_{iii} in Fig 6). As grazing intensities are reduced further (between G_{ii} and G_i), we expect conditions where both Brome and native perennial populations can persist, neither can invade each other, and both can invade Medusahead populations established at this grazing intensity. Lastly, in areas that are ungrazed or with very low grazing intensities, we predict that only native perennial grass populations (P in Fig. 6) will persist and that native perennial grasses will be able to invade the other established populations.

H3: ***Pathways of rangeland degradation will be different than pathways of recovery***. Rangelands that change states in response to a small increase in grazing intensity will not be reversible by an equally small reduction in grazing intensity. For instance, a small increase in grazing at already high grazing intensities (e.g, to just past G_{iii} in Fig. 6) should allow Medusahead (A2) populations to invade Brome (A1) populations, yet a reduction in grazing intensities in a Medusahead-dominated pasture will not allow the invasion of Brome until grazing intensity is reduced to much lower levels (e.g., below G_{ii}). We would expect similar dynamics in the conversion and recovery between native perennial and Brome populations.

Tests of H3 (hysteresis). To test our third hypothesis, we will compare conversions to different states in pastures that are initially heavily-grazed and moderately-grazed as we manipulate grazing intensities. Hysteresis would be indicated if the pathway of dominance of Medusahead (Medusahead is predicted to invade the Brome dominated pastures in the high grazing manipulation) is different than the pathway of recovery to Brome dominance in the heavily grazing pastures (Brome is predicted to invade the Medusahead dominated pastures at intermediate levels of grazing).

H4. ***Positive feedback mechanisms maintain rangeland states.*** Positive feedback should maintain the persistence of alternative states. We hypothesize that two mechanisms will be particularly important in these rangelands: a) microbially-mediated feedbacks where a plant species impacts the microbial community to its own benefit; and b) resource-mediated feedbacks where a plant species impacts nutrient cycling characteristics to its own benefit (e.g., through litter quality or resource use patterns).

Tests of H4 (positive feedbacks). We will test these mechanisms across manipulations of grazing intensities in the communities where the different species groups were established following solarization. We will use soil "cultured" in each of these species-grazing treatments in a greenhouse phytometer experiment to determine the effect of microbial community on the performance of the three species groups. To test for resource-mediated feedbacks, we will monitor the effects of plant species composition on nutrient cycling and response of these species groups to the different soil resource conditions.

IV. EXPERIMENTAL APPROACH

We will conduct the proposed work at the Sierra Foothills Research Extension Center, a University of California Agriculture and Natural Resource Center north of Sacramento. This is the site used by George et al. (1992) for their state-and-transition model (Fig. 1), and has pastures that contain the necessary rangeland states our study will address. The Center has multiple pastures that have been maintained at different grazing intensities for over 20 years. We have worked at this site previously and have received informal support for this current proposal from the site manager.

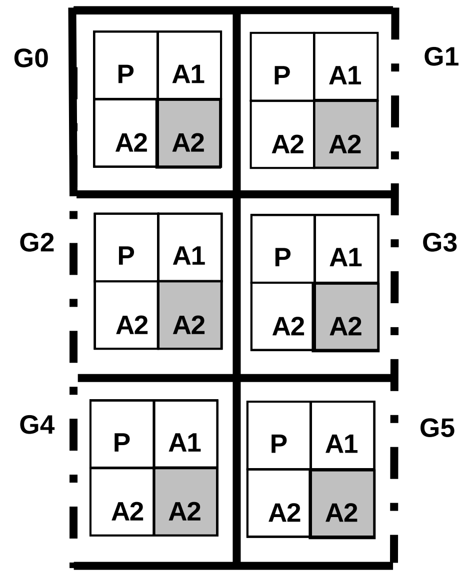

Figure 7. Experimental split plot design. We will establish six levels of grazing intensity, ranging from ungrazed (G0) to heavily grazed (G5). Solid lines indicate permanent fence and dashed lines indicate temporary fence that can be opened and closed to achieve desired grazing intensity. Seedling and solarization treatments are nested within grazing treatment (P=perennial grass, A1=desirable annual grass, A2=noxious annual grass). Shaded subplots are intact communities (no solarization); in this schematic we show a pasture initially dominated by Medusahead (A2). Unshaded plots are solarized to eliminate seed bank and reduce influence of species-specific microbes. After solarization, we will add seeds of the designated species groups. Subplots are 20m x 20m and entire block is ~1ha. Treatments will be randomly assigned and blocks replicated in 8 separate pastures of ~10-15 ha – four dominated by A2 and four by A1.

A. Field Experimental Design. Our experimental design will consist of eight replicate fenced exclosures established in existing grazed pastures (10-15 ha): four in existing pastures dominated by Medusahead and four in pastures dominated by acceptable forage annuals (e.g., Brome species). Each block will be divided into 6 plots which will receive one of the six grazing level treatments. Grazing levels will be achieved by strategically opening and closing of the temporary fence lines (Fig. 7). The four solarization/seeding treatment subplots (20m x 20m) will be randomly nested in each grazing level (see below and Fig. 7). We will also maintain a 2m x 2m bare ground subplot to characterize soil resource measurements in the absence of plant species for use in parameterizing our mathemeatical models (see section IV-C).

Grazing. We will experimentally manipulate grazing intensity to understand its role in the transition between annual and perennial grasslands. We will apply six levels of cattle grazing intensity in the exclosures by opening the sides of each exclosure for appropriate lengths of time to achieve target grazing levels. The exact time will vary depending on the phenology of the site and the weather conditions of the year (George et al. 2002, Kimball and Schiffman 2003).

Our target grazing levels will be based on adjacent actively managed pastures. Residual Dry Matter (RDM; the old plant matter left standing at the start of the growing season) is widely used by land management agencies as a standard of grazing use on rangelands (George et al. 2002). Grazing intensities will range from the ungrazed treatment (expected RDM 1500-1800 lbs/acre at this site) to the most heavily grazed treatment (RDM ~15% of ungrazed, 200-300 lbs/acre, based on previous estimates of an intensely grazed rangeland property bordering our site). We will measure RDM, aboveground standing biomass and belowground biomass (see Table 1) to document grazing treatments as well as the effects of the different species groups.

<u>Solarization/seed addition</u>. We will focus on three groups of species: the native perennial grasses *Nassella pulchra* and *Elymus glaucus* (P); the exotic annual grasses that are acceptable forage *Avena fatua* and *Bromus hordeaceus* (A1); and the noxious annual grass *Taeniatherum caput-medusae* (A2, Medusahead).

We will establish populations of each of these species groups in all the pastures and grazing treatments (Fig. 7). To eliminate priority effects, we will solarize the soil in three of the four 20m x 20m subplots in each of the grazing treatment plots during late summer and fall of the first year of the project. We will also leave one subplot where we do not solarize (shaded box in Fig. 7). Solarization involves laying sheets of clear plastic over freshly tilled soil. Edges will be buried to produce a heat trap, killing seeds and some microbes (Hartz et al. 1993, EPA 1996, Schultz 2001). Following solarization and at the beginning of the winter growing season in year 1, we will sow seeds of the three groups of species, one group in each of the solarized subplots. Seeds will be sown at a rate of 10 g/m^2 and perennials will be both broadcast and no-till drill-seeded to maximize establishment. We have had success establishing native perennial grasses in a previous experiment, even without drill-seeding (Seabloom et al. 2003b). The plots will be treated with a broadleaf herbicide during the first year to minimize invasion by exotic forbs such as *Brassica nigra*. Plots will be allowed to establish without grazing for two seasons, and then subjected to grazing treatments starting in the end of the second growing season.

<u>Reciprocal Invasions</u>. At the beginning of the first growing season (in half of each unsolarized subplot) and at the beginning of the third growing season (in the other half of each unsolarized subplot, as well as the solarized subplots), we will broadcast sow seed of each species group into all of the subplots at a low rate ($1g/m^2$) to test the reciprocal invasibility criterion. Seeds from all species except Medusahead are available through a regional seed company; Medusahead is abundant at our site and will be collected on-site.

Specific results that would support hypothesis 1: Persistent States.
To test our first hypothesis, we will concentrate on grazing manipulations in the unsolarized subplots (shaded subplots in Fig. 7). These manipulations will occur in two types of pastures: in initially heavily grazed pastures dominated by Medusahead (A2) and in initially moderately grazed pastures dominated by acceptable forage annual species (A1), for a total of 48 plots. We will monitor species composition, and aboveground and belowground production (see Table 1 for details) starting in year 1 of these plots. In years 1 and 3, we will add the propagules of our three focal groups: noxious annuals, acceptable forage annuals, and native perennial grasses. We will measure invasion success in years 1-4 (see Table 1 for details). These manipulations will allow us to test whether the original dominant of the pastures (Medusahead in heavy grazed and Brome species in moderately grazed) will be relatively resistant to the invasion of the other groups, and able to persist across a range of grazing intensities (Fig. 8). Alternatively, if the climax-succession-retrogression

model is supported, we should see Needlegrass abundance increase linearly as a function of grazing intensity into both Brome and Medusahead pastures, and similar linear patterns for Brome invasion into Medusahead pastures. To statistically test H1, we will analyze invasion success (abundance or population growth rate) with an ANOVA model with pasture type (2 levels) and grazing (6 levels) as fixed factors and preplanned contrasts to test for differences in threshold effects (Fig. 8).

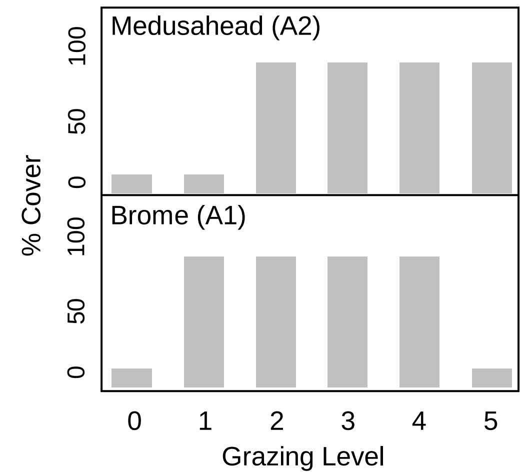

Figure 8. If states are persistent then we expect to find that the original dominant in the pastures (Medusahead in heavy grazed or Brome in moderately grazed pastures) to be able to persist across a range of grazing intensities in the non-solarized plots in the presence of alternative species groups added as seed.

Specific results that would support hypothesis 2: Divergence.

We will follow species composition in the solarized subplots where we will sow the three species groups (P, A1, A2), let them establish, and then expose them to a gradient of grazing intensities. In year 3, we will invade with the other species groups. We will follow invasion success (see Table 1) in these manipulations to test whether alternative rangeland states can exist dependent on initial conditions. At each level of grazing intensity, we will test whether: 1) the species group was able to establish when it was originally sown after solarization in year 1; and 2) the other species groups were unable to invade it (i.e., not have a positive population growth rate) when added in year 3. If both these criteria are met, we will consider the species group a stable state at that level of grazing intensity. If two species groups meet the criteria at the same level of grazing, we will consider this support for the existence of multiple stable states (Fig. 9).

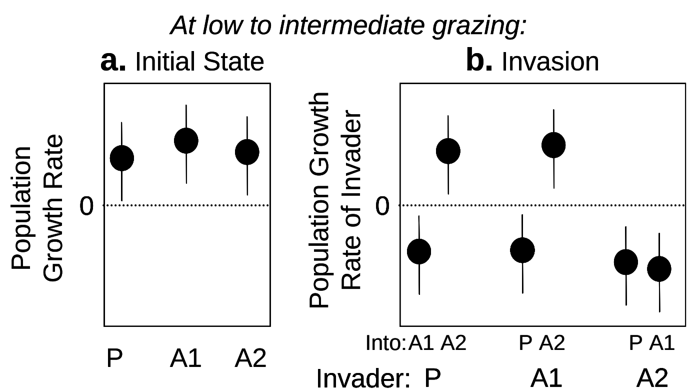

Figure 9. a) Alternative stable Needlegrass (P), Brome (A1), and Medusahead (A2) states will exist depending on initial conditions. Populations of each state will maintain positive growth rates when established on solarized soil. **b)** These alternative states will not be invasible, e.g., the population growth rate of Needlegrass (P) will be negative when added to established populations of Brome (A1) but positive when added to unstable Medusahead state (A2). We expect similar results for Brome and Medusahead as alternative stable states at high to intermediate grazing levels (between levels G_{ii} and G_{iii} Figure 6).

Specific results that would support hypothesis 3: Hysteresis.

Here, as in Hypothesis 1, we will concentrate on grazing manipulations in the unsolarized subplots (shaded plots in Fig. 7) that will be conducted in two types of pastures ... y Medusahead (A2) and initially moderately grazed past... treatments where we manipulate grazing intensities ar... between the two pasture types. Hysteresis would be i... successfully invade the Medusahead pasture is differe...

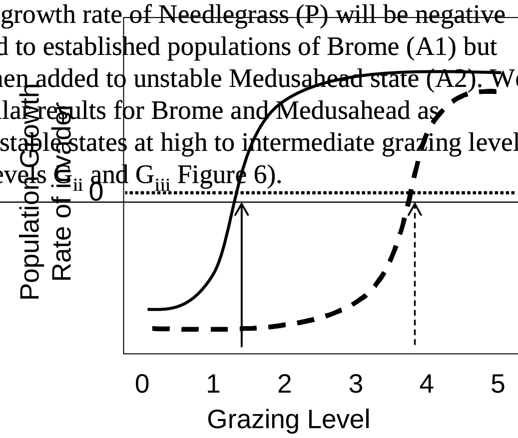

Figure 10. Invasion of Brome into Medusahead (solid line) differs from invasion of Medusahead into Brome (dashed line); arrows correspond to thresholds.

Medusahead can successfully invade the Brome pasture. To statistically test this hypothesis, we would examine invasion success as a function of three factors (species, grazing intensity and pasture type) in an ANOVA model with preplanned contrasts testing whether the grazing level threshold for Brome differs from that of Medusahead (and similarly for Needlegrass) (Fig. 10, response shown as continuous function of grazing level for clarity).

B. Plant-soil Feedback Experiments. We will take two approaches to investigate the role of plant-soil feedbacks. First, we will use soil from the field experiment (above) to characterize the effects of species on nutrient cycling and soil microbial communities ("full soil"). Second, we will conduct a soil culturing experiment to determine the effects of the soil microbial community on plant growth and survival ("soil training").

Field measurements and microbial community characterizations. To document species resource impacts (as well as the effects of the grazing treatments), we will measure inorganic nitrogen availability, microbial biomass N, water availability, and light availability (Table 1) in each subplot. To describe soil microbial communities, in year 3 we will collect rhizosphere soil and measure fungal and bacterial community composition across a range of grazing intensities and dominance states (see Table 1 for details). To characterize mycorrhizal infection associated with each of these species, we will quantify percent colonization in root samples (taken from the same cores as the rhizosphere soil, above).

Greenhouse feedback experiments. We will conduct a soil feedback greenhouse experiment in year three. This experiment will consist of two parts. First, we will examine the growth of the focal species in rooting depth soils collected from field experiment ("full soil" experiment). In year three, we will collect a substantial amount of soil from the three types of species groups (in initially solarized plots) from three levels of grazing intensity. All the soil types (the native perennial grasses (P); the exotic annual grasses (A1); and the noxious annual grass (A2)) from the three levels of grazing intensity (G0, G3, G5) will be added to cone-shaped pots (3 cm diameter, 10 cm deep). We will plant seeds of the three species groups in each of eight replicate pots of the soil types (216 total pots).

Soil effects could differ because species differ in their effects on nutrient cycling or in their effects on the microbial community. Thus, secondly, we will examine the specific effects of an altered microbial community by conducting a “soil training” experiment (Bever 2003). We will add collected rhizosphere soil as inoculant to pots with sterilized soil (collected from the field site) in a 40:1 soil to inoculant ratio. We will create 24 replicates of five treatments: 1) sterile soil plus native perennial grass innoculum; 2) sterile soil plus exotic annual grass innoculum; 3) sterile soil plus noxious annual grass innoculum; 4) sterile soil (no inoculum); and 5) non-sterile soil (no inoculum). The unsterilized control is included because steam sterilization can lead to a flush of nutrients. Seed of the three species groups will then be added to eight pots of each of the five treatments (120 pots).

For both the “full soil” and the “soil training” experiment, pots will be randomized and watered daily. When seedlings emerge, they will be thinned to one seedling per pot. Foil will be used to cover the soil surface and minimize cross-contamination. After three months, plants will be destructively harvested for aboveground and belowground biomass. Results for each species will be analyzed with analysis of variance techniques.

Table 1. We will measure a broad range of community and ecosystem responses in the field experiment. These will be used to test our hypotheses and parameterize our models.

Measurement	**Why?**	**How Measured**
Residual Dry Matter; Aboveground Net Primary Production	Document grazing effects on ANPP	Clipping end of dormant season (RDM) and peak season biomass (ANPP), dry at 60^{o}C for 48hrs and weigh. Small strip harvests (1m x 10cm) annually.
Belowground production	Document treatment effects belowground	Root ingrowth cores (2cm diameter) harvested years 3 and 4 (Robertson et al. 1999).
Community composition; Invasion success	Predict longer-term population growth rates, describe treatment effects on community composition, and identify species specific responses.	Census tagged individuals twice annually to quantify growth and mortality. Stem counts and point quadrat frame sampling (100 pts/m^2) to nondestructively estimate percent species cover (Gibson 2002).
Reproductive output	Characterize propagule production.	Collect seed from 50 stems per species per treatment subplot at the end of growing season, count and weigh.
Soil moisture, nitrogen availability, litter quantity and C:N ratio, water use efficiency (δ^{13}C).	Characterize treatment effects on soil characteristics, resource and litter feedbacks, parameterization of model (see Fig. 9)	Soil moisture probes in each treatment subplot, TDR measures 3 times during peak growing season, yrs 2-4. Ion-exchange resin bags, 10 cm depth, each growing season. 30-day *in-situ* mineralization rates, buried bag method with 10cm deep cores, year 3. Microbial biomass with fumigation-extraction techniques (Robertson et al. 1999). Collection of litter year 3 to determine C and N concentration and detla ^{13}C. For all soil measures, five samples will be taken from each subplot and composited for extraction.
Soil Microbial Characterization	Determine whether species groups influence the composition of microbial groups	Rhizosphere soil from a subset of plots in yr 3, extract Microbial DNA using phenol-chloroform extraction (Griffiths et al. 2000). Generate a microbial fingerprint using T-RFLP by amplifying 16S rDNA using bacterial primers F27 and R1492 and fungal 18s rDNA using fungal-specific primer set EF4/EF3 (Smit et al. 1999).
Mycorrhizae Characterization	Characterize effects of treatments on mycorrhizal colonization.	Roots will be soaked in 50% EtOH, cleared in KOH, and stained with 0.03% Chlorazol Black E in lactoglycerol.

Specific results that will support hypothesis 4: Positive feedbacks. Positive plant soil feedbacks would be demonstrated if plant species perform (grow, survive) better in pots containing their own monoculture soil or inoculum and perform worse in soil or inoculum associated with other species. Plant performance should be correlated to changes in nutrient cycling (field measures, Table 1) or microbial community (molecular characterizations, Table 1). Comparison of the "full soil" with the "soil training" experiments will indicate whether feedbacks are mediated by alterations of nutrient cycling and/or whether they are specifically mediated by the soil microbial community. Alternatively, negative feedbacks would suggest coexistence processes rather than multiple state dynamics.

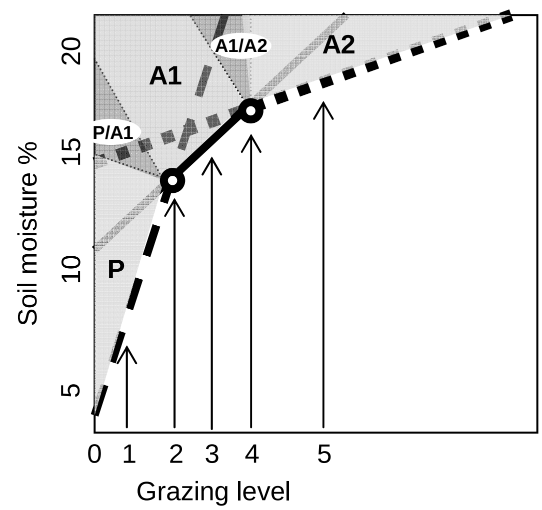

Figure 11. Graphic version of basic model (Fig. 12a) representing a grazing dependent hierarchy in competitive ability for water. Native perennial grasses such as *Nassella pulchra* (P) dominate at low grazing levels provided seed limitation is overcome. With increasing grazing intensity *Bromus hordeaceus* (A1) and then *Taeniatherum caput-medusae* (A2) dominate. Stable or unstable coexistence (circles and dark gray shading) depends on relative resource and grazing impacts of the species. Lines are the zero net growth isoclines for P (dashed), A1 (solid), and A2 (dotted). Positive growth rates occur above and to the left of isoclines.

C. Consumer-Resource Models.

We will develop a set of differential equation models to explore the sensitivity of this system of grasses to herbivory (e.g., Fig. 11, a graphic representation of a three species, one resource, and a shared consumer model). We will parameterize these models using our experimental results. In general, we predict that transitive and inverse hierarchies of competition for a limiting resource and response to a predator can produce alternative outcomes that are dependent on resource supply and grazing intensity, with some combinations of species never coexisting. We expect that perennials should exclude annuals when competing for limiting resources such as water and nitrogen when grazing intensity is low but would be competitively excluded at higher grazing levels (Fig. 11). Conditions of unstable coexistence with positive feedbacks should promote alternative state dynamics that are analogous to our predicted field experiment results.

The theoretical framework we use builds on and extends a previously described model of competition between two plant species for a shared resource and a shared herbivore (Fig. 12a) (Holt et al. 1994, Grover 1997, Chase and Leibold 2003). This basic model can be described by a set of differential equations:

$$dH/dt = H(\sum(m_i c_i N_i) - d_H)$$
$$dN_i/dt = N_i(f_i a_i R - m_i H - d_i)$$
$$dR/dt = \mu[S - R] - \sum(f_i N_i)$$

in which H represents the generalist herbivore which is shared by the N_i different plant species (P, A1, and A2 in our field experiment; i=3 in this case) competing for the limiting resource R, m_i is the feeding rate of the herbivore on plant N_i and c_i the corresponding conversion efficiency. The herbivore has a loss rate *d*. The plants consume the resource at rate *f* with a conversion efficiency *a*; they are lost at rate *d* and also by herbivores at rate *m*. Resources are supplied at rate c from the unused resource pool *[S-R]*, where *S* is the total supply pool. This model treats resources as an internally fixed pool which would hold for resources like nitrogen but is not realistic for a resource like water. We use this basic model as a first approximation of general resource competition and will then modify the resource dynamics to reflect externally driven water supply and transpiration loss by plants (Fig. 12a). This basic model can produce the case of multiple stable states for certain sets of parameter values (Chase and Leibold 2003) and thus qualitatively satisfies our first three hypotheses tests. It will allow us to explore the sensitivity of the model parameters and their degree of concordance with field results. We can then extend this model and explore how hypothesized positive feedback mechanisms (Hypothesis 4) change regions of instability and the resilience of alternative stable states (Fig. 12b&c).

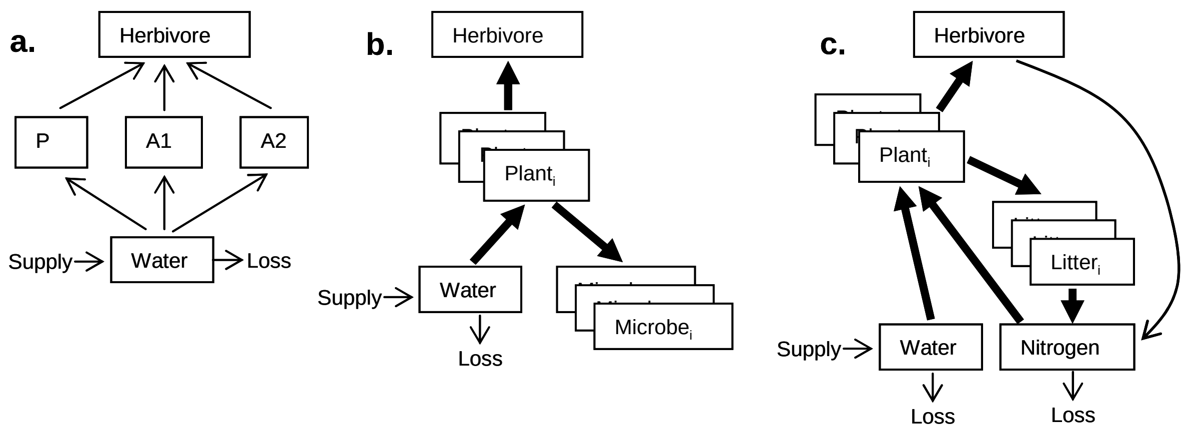

Figure 12. **a)** Basic three level consumer-resource model representing our system of native perennial grasses (P), acceptable annual grasses (A1), and noxious weeds (A2). Arrows show transfers of biomass/resources. Extended model versions: **b)** Addition of microbes (pathogens and/or mutualists) that differentially favor each plant species. For simplicity, stacked plant and microbe trophic groups represent different species groups (e.g., P, A1, A2). **c)** Addition of litter feedback. Litter from each plant species differs its rate of decomposition (conversion into inorganic N) which also depends on water availability. Again, for simplicity, stacked plant and litter trophic groups represent different species groups. Bold arrows between plants, microbes, water, N, and herbivore indicate that each plant species has unique resource and consumer parameters.

We will extend the basic model by adding soil microbes (Fig. 12b) as an additional set of shared consumers that have differing impacts on the different plant species, thereby allowing us to explore effects of positive feedback on local stability and resilience of alternative states (Hypothesis 4). These additional consumers could act as either pathogens or mutualists depending on the sign of their impact. We also extend the basic model by adding nitrogen as an additional resource whose biological coupling with water can create positive feedback effects (Fig. 12c). A similar version of this model extension (but without herbivory) has been shown to result in multiple stable states (C. DeMazancourt, personal communication). This extension of the basic model will let us explore the role of litter quality differences in driving a positive feedback. Multiple stable states will be assessed through stability analysis and the criteria of non-mutual invasibility. The basic model (12a) is analytically tractable whereas the extended versions (version **a** with realistic water dynamics and **b** and **c**) will be solved numerically in MATLAB.

We will parameterize the above theoretical models using data collected from our experiments. For example, differences between soil moisture over time in the species treatment subplots and bareground subplots will provide a quantitative index of species-specific resource use rates, periodic biomass harvests can provide indexes of loss to herbivory, tissue C:N and $\delta^{13}C$ are indexes of nitrogen and water use efficiencies, and mineralization rates can be used as indices of N supply rates. Parameter estimates will be supplemented as necessary from the literature: many parameters including litter decomposition, growth rate, plant loss rate (leaf longevity) and resource use patterns have been shown to correlate strongly with simple leaf chemistry measurements such as tissue N (Reich et al. 2003). Experiment-specific models will be developed and results compared with experimental results as tests of model validity.

D. Addressing potential weaknesses. There are obvious limitations to exploring threshold ecosystem dynamics empirically. By being broad and trying to encompass several types of dynamics, it is inevitable that some components are less developed than others. We have tried to anticipate and address this proposal's weaker aspects. Our goal is not to provide rationale for the experimental design but to point to necessary compromises in this work.

It is important to note that shorter-term dynamics may not predict long-term dynamics, particularly if local and global stability differ. Both the initial establishment of alternative communities and their subsequent exposure to experimental grazing levels are fairly short (2 years each). The time required for perennials to establish and produce significant ecosystem impacts, to generate positive feedbacks, and for grazing to have significant effects may be longer than this. However, in a previous experiment we were able to establish subplots significantly dominated by native perennial grasses within two years and the results shown in figures 3-5 were all from this experiment (Seabloom et al. 2003b). In the time frame of this proposed work, we necessarily concentrate on shorter-term ecosystem responses. Moreover, the design of this experiment will allow us to extend our investigation over a longer timeframe; we will seek future funding to permit us to do so.

Second, it is clear that more factors than invasion and grazing influence the health of California rangelands. We address a handful of factors where evidence indicates they could be related to transitional mechanisms. We do not address fire, although burning is a management technique and shown to be important in these systems. We also do not address the intricacies of grazing management here. We feel that this design is already quite complex and the addition of other factors will make the approach unwieldy and not applicable in a management context. We hope this project will serve as a model that will guide the exploration of how these other factors may drive state transitions.

Third, California rangelands could be considered unusual in terms of their invasion and transition dynamics. California rangelands are somewhat of an anomaly for western US range management: they have been dominated by annuals for over two centuries and have little problem with shrub encroachment (Scholes and Archer 1997). However, over 60% of California is rangeland and about 80% of these rangelands are managed by state and federal agencies. These systems are an important contributor to state and regional economies, and also have very high conservation value (Wilcove et al. 1998). In addition, grassland Mediterranean systems are among those most vulnerable to global environmental changes (Jackson et al. 2000), changes which can act as exogenous drivers of system collapse. Although actual rangeland states will vary across ecosystems, this project will test an approach to advance management frameworks in general.

Fourth, it is important to recognize that there have been few empirical tests of thresholds and ecosystem states in the manner we propose. While this carries with it inherent risks, there are two reasons why we feel that the risks are particularly well justified for this research. First, there is widespread pattern-based evidence and agreement among resource managers that these rangeland systems generally behave as if governed by multiple state dynamics. Second, California rangeland systems are perfect to use the most widely accepted empirical approaches to test for these dynamics: species are easy to establish from seed, dyanamics are rapid, and ecosystem impacts relatively strong. We understand the recruitment and resource requirements of these species from past work. The experimental techniques proposed are feasible and practical.

V. PROJECT MANAGEMENT AND TIMETABLE . We are familiar with the proposed experimental techniques, vegetation and soil measurements, and have experience in the empirical analyses (Suding and Goldberg 2001, Seabloom et al. 2003b, Suding et al. 2003, Suding et al. 2004b). S. Harpole has substantial modeling skills, with experience in complex dynamics as well as extensive field experience with grasslands in southern California. Due to the nature of the field work associated with this project, we will also hire a project manager/research technician to work part-time on this project. For this position, we will seek someone with experience and interest in restoration and management of exotic grassland systems.

We request funding for four years, although we intend for the project to last longer-term (Table 2). In the first year, we will set up experimental plots (solarization, seed sowing). We will begin grazing treatments at the end of the second growing season, but will monitor ecosystem responses beginning the first season through the end of the fourth growing season. In the start of the third growing season, we will add additional seeds to test invasion success. In the final year, we will complete data analyses and prepare results for publication. We will disseminate information via publications and presentations in management and academic research venues, and will make all data accessible via a website in a timely manner (1-2 yrs after collection). We will pursue opportunities to present seminars to local rangeland managers as well as nationally and will encourage other researchers to use the experimental set-up to ask related questions not covered here (e.g., genetic, microbial, insect responses).

VI. SIGNIFICANCE AND IMPLICATIONS.

We have made great progress over the last decade in bridging the gap between abstract theory and ecosystem dynamics in natural systems (Foley et al. 2003, Peterson et al. 2003). The success of conservation and restoration efforts will depend heavily on our understanding of threshold dynamics and the sensitivity of natural systems to environmental change (Carpenter et al. 1999, Suding et al. 2004a). The application of state and transition models in rangeland management is exemplary of this progress, but lacks mechanistic tests posed in the framework of a general explanatory theory.

Because neither field patterns nor models alone can be conclusive, it is crucial to experimentally identify what factors make a system cross a hard-to-reverse threshold. This work will validate and refine state and transition models, aid in the development of management frameworks, and test assumptions about the restoration of native perennial rangelands. We investigate if, and how, overgrazing can change resilience and thresholds in these systems. We will disseminate this information widely and make our data and experimental manipulations accessible to all interested parties.

Table 2. Timeline and Responsibilities. Tasks will be performed by the following people: KS (Katharine Suding), SH (Stanley Harpole, postdoctoral researcher), RT (Research technician, to be named), RM (Reserve managers), ALL (all members of the research team). Proposed funding will start September 2006, although we plan to do some preparation work prior to the start date.

Task/Responsibility	Who?	06/06 09/06 03/07 09/07 03/08 09/08 03/09 09/09 03/10	
Study Preparation			
Select pasture locations	KS, SH	XXX	
Finalize permission	KS	XX	
Order equipment	KS	XX	
Collect seed	SH, RT	XXXXXXXXX	
Prepare for Manipulations			
Establish plots, solarize	KS, SH	XXXXX	
Install fences	SH, RM	XX	
Install plot instrumentation	KS, RT	XX	
Baseline measurements	ALL	XXXX	
Manipulations			
Manipulate grazing	SH, RM	XXXXXXXXXXXXXXXXXXXXXX	→
Add seed	SH, RT	XX	→
Reciprocal invasion	SH, RT	X XX	
Ecosystem Response Measures			
Field measurement (Table 1)	ALL	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	→
Lab analyses of samples	RT	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	→
Feedback Mechanism Tests			
Whole Soil experiment	SH, RT	XXXXXXXXXXXX	
Soil Culture experiment	SH, RT	XXXXXXXXXXXX	
Data Analysis and Synthesis			
Model dev/parameterization	KS,SH	XXXXXXXXXXXXXXXXXXXXXXXXXX	
Analyze data	KS, SH	XXXXXXXXXXXXXXXXXXXXXXXXX	→
Prepare publications	KS, SH	XXXXXXXXXXXXXXXXXXXXXXX	→

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