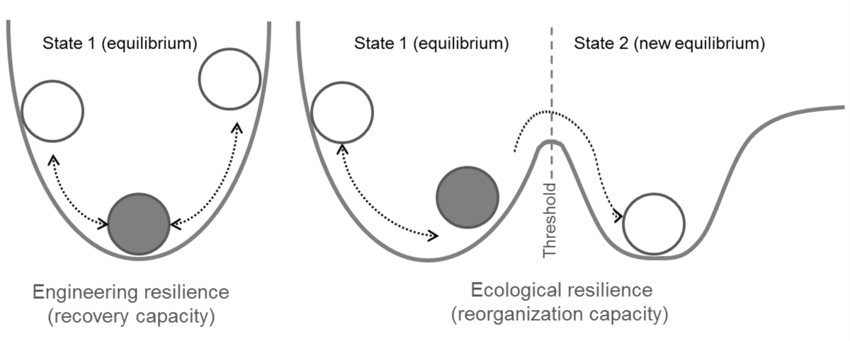
**State Change Outline:**

* Introduction to annual grasslands:
  + History of the three groups of species in annual grasslands
    - Natives
    - Naturalized annuals
    - Invasive species
  + Annual grasslands as a system
    - No clear patterns of succession, even in the absence of:
      * Grazing
      * Fire
      * Any consistent disturbance?
  + However, this lack of succession does not mean that species composition is “fixed”
    - Dramatic shifts in plant communities are thought to be mediated by year-to-year climatic variation.
    - Invasibility / resilience thought to differ between community “types”. High resilience of established native communities, low colonization ability. Annuals vs. WAPs, etc.
    - Annual life history places a ton of emphasis on seedling dynamics – communities dramatically thin themselves after germination. Between 1-10% of the total community survives to peak productivity. Low seed longevity, little seed bank in annuals.
      * Droughts, particularly longer-term events, can have large effects on:
        + Seed production
        + Seedling survival (particularly sensitive to seasonal patterns)
        + Competitive interactions
      * Effects of single-year vs. lagged effects – rainfall patterns can have legacies
* State-change models:
  + To make sense of these fluctuations in annual rangelands, land managers have often turned to state-change models:
* 
  + In these models, managers attempt to categorize communities into discrete “states”, represented by the ball on a surface. Transition between states is moderated by some force that “pushes” the ball in different directions. The stronger the force, the more the ball is pushed. The more resistant a state is to some change, the deeper the “cup” in the surface.
* While these models are great conceptually, they can be hard to put into practice when analyzing data, particularly when we are considering multiple state types.
  + Reliance on “expert models” which are based on qualitative observation by land managers / consistent observers of the environment, rather than a more quantitative approach.
    - California grasslands are often divided into different “types”, largely based on introduction history or economic importance.
    - Clearly, timing of introduction does not necessarily reflect ecological function or a species “role” in the community.
  + Recently, a few approaches to developing state-transition models have appeared, which utilize classification techniques to “discover” states within the total amount of variance of community composition observed.
    - Citations:
      * Stein et al. 2016
        + State-change dynamics as a function of grazing intensity at SFREC.
        + Focused on role of residual dry matter in predicting frequency of state change and reciprocal invasions

No evidence that reciprocal invasions had a big effect

Transitions to a “forb” functional group (native, annuals, taeniatherum planted) were most common as a function of increased grazing intensity.

* + - * + Emphasis on an “increase when rare” criterion for coexistence and state change. Conceptually makes sense, but I don’t understand how it’s implemented in the model.
        + Model – logistic regressions of transition probability as a function of residual dry matter
      * Bagchi et al 2008
        + State-change dynamics and testing of an expert model in aridlands in the Southwest.
        + Model-based clustering of different states in a 70 year dataset of transects – emphasis on comparing the results of modelling with those of consensus expert models.

What species are expert models overestimating / underestimating the importance of in general vegetation dynamics?

* + - * + Somewhat less quantitative explorations of how environmental covariates drive transition patterns and frequency.
  + While these models have shown some similarities in approach (neat use of clustering algorithms), they don’t tend to really capture the elements of the state change model in their model.
    - For example, focusing on numbers of transitions vs. precipitations is interesting, but what if a state is transient? Little ability to distinguish between raw transition probabilities and the role of environmental covariates.
    - Solution: multi-state (or Markov) models! Used frequently in biomedical science. How do states of an individual (person or community) change over time? Often describe disease dynamics, where an individual progress from healthy -> vulnerable -> sick -> dead, but can often reverse between stages.
* We can “test” how well the expert states capture relevant variation in this system by providing propagules in a fashion that follows expert states, then examining how well these designations explain overall community variance.
  + Examining what states appear to form with different propagule treatments, and how these states fluctuate between one another can shed light onto the ecological interactions that are hypothesized to control patterns of community turnover in this system:
    - Priority effects and bottlenecks at establishment.
    - Differing environmental tolerances
* Using this state and transition framework, we aim to ask a number of different questions:
  + What defines states within California grasslands? Following the “narrow” definition of state-transition models, states are defined by delineations that best capture the range of vegetation cover. What are these states? How well do these states correspond to more traditional definitions of communities in annual grasslands?
  + Are transitions between states characterized by continuous, reversible changes (i.e. all communities can move between all groups) or non-reversible changes?
  + What governs transitions between states? Are some states more stable than others? Are transitions random, or the result of some environmental correlation?
  + (For discussion) What can these transitions tell us about the dynamics governing community interactions in California grasslands? How can we use this information to restore and manage these systems?

**Analyses:**

1. What defines states? How well do these states follow those of “expert models”?
   1. Clustering analysis and indicator species analysis
   2. Qualitative comparison with expert models
2. Are transitions between states characterized by continuous, reversible changes, or non-reversible changes?
   1. Transition probability table
   2. Figure of state assignments by planting group over time
3. What governs transitions between states?
   1. Model selection with different covariates (priority and precipitation).
   2. Figures of stability probability with respect to precipitation patterns

**Interpretation:**

1. Contrasts between expert models and those that seem to best describe community variation.
   1. Rough agreement between the expert models in the sense that there was a split between natives / naturalized annuals / invasives. However, annual species were further subdivided into 2 groups
      1. Makes sense, given the diversity of this species group
   2. Defining species of these groups:
      1. StiPul/ElyGla
      2. LolMul/Trifolium/VulMyu
      3. TaeCap/AegTri
      4. AveFat/BroDia/Leymus
2. Transitions were generally all reversible, **but governed by a series of covariates related to planting composition and environmental data:**
   1. Communities rarely transitioned to the native perennial state when these were not planted initially (low colonization ability)
   2. Some annuals did very well early on, but these failed to reappear after petering out – low community stability. Not as good competitively? Do these species rely on disturbance / priority to maintain themselves?
   3. Transitions to and between WAPs and Dry Season specialists seemed governed by precipitation pattern. Wetter weather = better for invasive species, continued drought = better for more drought-tolerant taxa. Less of a role of priority – transitions are likely whether planted in the initial seeding mix or not.
3. Interpretation:
   1. Frequency of transitions and movement between states illustrates several key dynamics:
      1. Trade-offs between colonization and competitive ability illustrated by differences between priority focused annuals and native species.
         1. Some annuals able to establish themselves early on, but difficult to return to this state later on – rely on disturbances / opportunities to colonize new areas for population maintenance? Or different environmental conditions.
         2. Natives able to establish themselves early on, but it’s difficult to have these species become dominant parts of the community later on if they aren’t established first.
         3. WAPs and Dry-season annuals able to establish regardless of whether they were part of the initial planting mix, but frequency depends largely on climatic events.

**Other things to consider based on readings:**

* What are some of the biogeographic / soil resource characteristics that are correlated with state change?
  + Are transitions correlated with soil resource use efficiency?
* Incorporating clipping data into analysis? Grazing is often the focus of STMs – also valuable to repeat analyses with the WAPS+Natives+Annuals groups with all clipping treatments, fertilization, and rainout shelters.
  + May be quite straightforward to do a comparison of functional group abundances over time as a function of grazing and treatment. However, I think this is a separate manuscript.

**Citations**

* + Bestelmeyer et al. (2009)
    - “Although general concepts surround state-transition models and ecological sites (potential classifications) have received increasing attention, strategies to apply and quantify these concepts have not.
    - Recommends a series of 8 steps for the co-development of ecological sites and STMs:
      * 1. Creation of initial concepts based on literature and workshops
      * 2. Extensive, low-intensity traverses to refine initial concepts and to plan inventory
      * 3. Development of a spatial hierarchy for sampling based on climate, geomorphology, and soils
      * 4. Stratified medium-intensity inventories of plant communities and soils across a broad extent with large sample sizes
      * 5. Storage or refinement of concepts
      * 6. Model-building and analysis of inventory data to test initial concepts
      * 7. Support and/or refinement of concepts
      * 8. High-intensity characterization and monitoring of sites
    - Bestelmeyer makes in interesting divide between ecological site concepts and state-transition model concepts.
      * Ecological site concepts typically involve more edaphic features or general landscape characteristics
      * State transition model concepts are more centered on community characteristics – states are a suite of temporally-related plant communities and associated dynamic soil properties that produce persistent, characteristic structural and ecosystem function attributes.
        + **Greater emphasis is needed on soil properties / biogeochemical cycling**?
  + Briske et al. (2008)
    - “Focus of paper is to recommend conceptual modifications for incorporation in state-and-transition models to link this framework explicitly to the concept of ecological resilience”
    - Dynamics among states within communities can be driven independently or in combination by natural events – emphasis on the difference between stability as a feature of a state, or the results of some external process?
    - Ecological resilience as a definition – the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures.
    - “Community phases within a state are assumed to be readily reversible over relatively short time periods”. However, not all community phases have reversible connections, because an immediate pathway is required.
      * **Relevant to think of California grasslands as a set of different “states”? Or community phases within a broader grassland state, which is distinguished from oak savannah, chaparral, etc.? Is this STM framework better in more perennial grassland sites?**
  + Briske et al. (2005)
    - More synthesis of “the ecological concepts and perspectives underpinning the development and application of state-and-transition models, thresholds, and rangeland health.”
    - State-transition model arose from the inability of the standard range condition and trend analysis models to account for all of the vegetation turnover in rangeland sites.
      * Vegetation can be continuous and reversible, or discontinuous and nonreversible. Variables such as fire and weather can play an equal or greater role than grazing in vegetation dynamics Vegetation dynamics often possess more than one successional pathway and/or stable plant community on individual sites.
  + Allen-Diaz and Bartolome (1998­)
    - “State-change models have been proposed as a replacement for the classic linear succession model and its derivative Range Condition model for describing and predicting rangeland community dynamics in response to management.”
    - Range conditions models identify range sites/ecological sites as a kind of land with a specific potential natural community, specific physical site characteristics and response to management. “The approach has not always proven effective because of flaws in the linear successional model, a lack of clearer links between grazing and vegetation change, and difficulties in objectively delineating and identifying range sites.”
    - State-transition approaches seem particularly good when states are easy to define – in many cases, these seem to be more subjective or based on some sort of external criterion; rangeland value, for instance. **How do you define states when looking at ecological interactions / community composition, rather than economic value or general transitions?**
  + Reviewed in Stringham et al. 2003
    - Definitions of terminology used in state-transition models, discussion of the various components, states, transitions, and thresholds. Good resource for framework.
    - USDA NRCS adopted use of state-and-transition vegetation dynamics in describing rangeland ecological sites.
    - Conceptual models have often incorporated state and transitions and not always thresholds (shifts that are irreversible, or nearly so).
      * Broad interpretation – climate/soil/vegetation domains that encompass a large amount of variation in species composition. Focused on functional integrity and thresholds of self-repair.
      * Narrow interpretation – far less variation in plant composition. States are typically depicted as seral stages or phases of vegetation development. Focused on vegetation.
    - Emphasize that a state is a “recognizable, resistant, and resilient complex of 2 components, the soil base and vegetation structure. The vegetation and soil components are necessarily connected through integrated ecological processes that interact to produce a sustained equilibrium that is expressed by a specific suite of vegetative communities”.
  + Westoby et al. (1989)
    - One of the first to apply the use of state-and-transition terminology to non-equilibrium theory for the purpose of producing a management focused model that describes vegetation dynamics in a non-linear framework.