# LTER: Sevilleta (SEV) Site: Climate Variability at Dryland Ecotones

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#### **II. PROJECT DESCRIPTION: SEVILLETA SITE – CLIMATE VARIABILITY AT DRYLAND ECOTONES**

#### Rationale: Climate Variability as a Key Driver of Dryland Dynamics



Fig. 1. Scenarios of increases in the mean and/or variance of drought.

Anticipating the consequences of climate change is arguably the most pressing challenge at the interface of science and society. Not only is mean temperature increasing, but precipitation is becoming more variable (Fischer et al. 2013, IPCC 2013), Nowhere will the ecological impacts of these dual changes be stronger than in drylands, particularly at dryland ecotones, where species reach physiological and ecological limits (Allen et al. 2015, Anderega & Diffenbaugh 2015). Much prior ecological research on climate change has emphasized trends in mean climate variables or separate study of extreme events (e.g., Jentsch et al. 2007, Knapp et al. 2015, Malyshev et al. 2016). Yet, effective forecasts require determining responses to both non-stationary components of climate distributions: the mean and the variance (Fig. 1). We propose a new LTER program to address the question: How do changes in climate mean and variance independently and interactively affect the dynamics of dryland ecosystems and the transitions

**among them?** While we are certainly not the first to study the significance of variance (e.g., Benedetti-Cecchi 2003, Knapp et al. 2008), we are ideally positioned to transform understanding of this important ecological problem by using experiments, observations and models that integrate across scales.

Drylands worldwide are experiencing <u>biome transitions</u>: the expansion of some ecosystem types at the expense of others. These transitions include encroachment of  $C_3$  shrubland into  $C_4$  grassland (Eldridge et al. 2011) and conversion of woodland to savanna (Allen et al. 2015). It is through these transitions that the largest changes in dryland ecosystem processes are occurring (Anderson-Teixeira et al. 2011, Biederman et al. 2016, Sala & Maestre 2014). Climate change affects not only single ecosystems over time, but also the rate at which historically stable ecosystem types change to new states (Allen & Breshears 1998). While climate change is implicated in biome transitions globally, dynamics are often ascribed to change in mean climate. However, prior work suggests that climate variance could also have pronounced impacts at ecotones (Elliott 2012, McAuliffe et al. 2014) because species reach ecological or physiological thresholds (Jiang et al. 2016). At our proposed Sevilleta (SEV) site, ecotones among five major dryland biomes (Table 1) will yield powerful generalization to drylands worldwide.

Drylands are highly variable (Fig. 2), providing an excellent test bed to advance general theory on ecological responses to environmental variability. Climate models consistently forecast higher precipitation variance, even while long-run mean precipitation trends for US drylands are notoriously



Fig. 2. Temporal variability in above-ground net primary production (ANPP) for 24 global sites. SEV sites span the dryland range. D= dryland, G=mixed grassland, M=mesic grassland, F=forest, A=Arctic or alpine.

unpredictable (Garfin et al. 2014, Gutzler & Robbins 2011, Seager et al. 2007). Although some predict increased dryland primary production under higher aridity (Hufkens et al. 2016), such predictions are highly controversial and at odds with current data (e.g., Brookshire & Weaver 2015). Given these contradictions, long-term research addressing how changes in climate variance affect drylands is urgently needed.

Understanding the effect of climate variance on drylands also has practical global importance. Of all the land cover classes, arid and semi-arid ecosystems contribute most to inter-annual variability in global carbon flux due to their high year-to-year variability in primary production (Ahlstrom et al. 2015, Biederman et al. 2016, Huang et al. 2016a, Poulter et al. 2014) and large surface area (~40%), which is rapidly expanding (Huang et al. 2016b). Currently, we lack both empirical research and theory to link the consequences of climate mean × variance interactions over space, time, and levels of biological organization. We propose to develop this theory and generate long-term data to test it.

# Theory: Ecological Responses to Climate Variability

Advances in theory on the consequences of environmental variability have progressed largely independently in evolutionary biology (Bell 2010), population biology (Lawson et al. 2015), microbial ecology (Hawkes & Keitt 2015), community ecology (Chesson 2000), and ecosystem science (Rodríguezlturbe & Porporato 2004). Unifying these diverse concepts can yield new insights into mechanisms that link ecological responses to environmental variance across scales (Collins et al. 2014, Kissling & Schleuning 2015, Vazquez et al. 2016). In addition, a process-based understanding is critical to making realistic forecasts under future, no-analog conditions (Evans et al. 2013, Petchey et al. 2015).

#### Climate Sensitivity Functions.

Theory predicts that the effects of environmental variance, at any scale, depend on the shape of the climate sensitivity function (Fig. 3), which depicts the relationship between an ecological response, such as fitness or primary production, and its climate driver (e.g., annual precipitation). Sensitivity to change in climate mean is gauged by the magnitude of the linear relationship: steeper slopes signify greater sensitivity than weaker slopes. For example, Munson (2013) used linear functions to identify "climatic pivot points" at which species responses shift from increases to declines.

However, many responses to climate may be nonlinear. If the function is nonlinear, then changes in the variance of climate alone can drive the long-term outcome, even if mean climate does not change (Jensen's inequality, Pickett et al. 2015, Ruel & Ayres 1999, Turelli 1978). Concave (downward) functions (Fig.



Fig. 3. Climate sensitivity functions. Nonlinearity causes climate variance to affect ecological responses most strongly with decreases from the climate mean (concave: A), increases from the climate mean (convex: B), or both (C).

3Å) yield negative effects of increasing variance, because years with low values of the climate variable (e.g., dry years) cause large decreases in the response, while years with high climate values cause only small increases. In contrast, convex (upward) functions (Fig. 3B) cause positive effects of climate variance. For example, wet years can bring a responsive system above its climate threshold (Heisler-White et al. 2009, Thomey et al. 2011). If the function changes concavity over a range of climate (Fig. 3C), then climate variance could have positive or negative effects depending on the climate mean, because the mean and variance interact. These interactions could influence systems on multiple levels, from populations of foundation plant species to consumers at higher trophic positions, and ecosystem, biophysical and biogeochemical processes.

Confronting variance has dramatically transformed some ecological disciplines (Carpenter et al. 2015). For example, models of intraspecific trait variance alter predictions of population stability, competitive dynamics, and rates of speciation (Bolnick et al. 2011, Hart et al. 2016). Ignoring long-term climate variance could profoundly under- or over-predict ecological responses to climate change, depending on whether variance poses a net cost or net benefit (Fig. 3). Laboratory studies and process measurements over short time scales (e.g., Borken & Matzner 2009, Sponseller 2007, Vazquez et al. 2016) suggest that nonlinear responses are common. However, observing nonlinearity at inter-annual scales requires long time series over naturally variable climates or direct manipulation of climate variance. Thus, most studies cannot predict ecological responses to higher inter-annual climate variance (see Hsu & Adler 2014a). Proposed research will help to resolve the relative importance of climate mean and variance in regulating the structure and function of dryland ecosystems.

#### Mechanisms of Climate Sensitivity.

What factors control the shape of climate sensitivity functions? Answering this question would expand the ability to predict sensitivity in other ecosystems worldwide. Although little studied, we suspect that *traits*, *diversity, species interactions*, and *disturbances* could each influence the sensitivities of populations, communities, or ecosystems to climate. For example, rooting depth is a <u>trait</u> that may predict climate sensitivity. Shallower roots should produce a concave function if the large rain events that drive wet years mainly percolate to deep, inaccessible soils (Gherardi & Sala 2015b). Alternatively, a fast growth rate may allow plants to rapidly increase biomass when water is available, as in some C<sub>4</sub> grasses (Xu et al. 2015b). This trait could yield a convex function due to the larger gains from wet years than costs under drought. Populations or communities with a high <u>diversity</u> of traits, species, or genotypes may be more buffered

against climate extremes than those with low diversity (Hooper et al. 2005, Isbell et al. 2015, Reusch et al. 2005). High genetic diversity also increases the potential for evolution to affect climate sensitivity. For example, under greater aridity, natural selection for drought tolerance (Silvertown et al. 2015) could reduce costs of climate variance by minimizing the steep declines under drought that produce concavity. Climate variability generates temporally fluctuating selection, which can help to maintain the genetic diversity that buffers populations against environmental change (Bell 2010, Botero et al. 2015).

At the community scale, the aggregate climate sensitivity function of a plant or consumer assemblage may also depend on climate-induced shifts in species abundance. For instance, increased dominance by drought-tolerant species could reduce sensitivity. <u>Species interactions</u> may exacerbate climate sensitivities (e.g., interspecific competition for water) or buffer them (e.g., interspecific facilitation via hydraulic lift). <u>Disturbances</u>, such as fire or nitrogen deposition, could also modulate climate sensitivity (Levine et al. 2016). For example, in wet years, plant resource limitation can shift from water- to nitrogen (Ladwig et al. 2012), creating concavity in the function. If chronic nitrogen inputs eliminate concavity by relieving nutrient limitation, this altered function would have lower costs of climate variance. Few have studied the factors that determine climate sensitivity functions (reviewed by Lawson et al. 2015, Vazquez et al. 2016). **Our research will push the frontier of global change ecology by developing general predictions of the mechanisms that cause ecological sensitivity to climate variance and mean.** 

#### Environmental Stochasticity and Antecedent Effects.

In addition to its influence via nonlinear sensitivity functions, increased climate variance can magnify the role of <u>environmental stochasticity</u>, or the randomness of climate events. While contributions to climate variance can be deterministic or stochastic, climate typically has a large stochastic component. Models show that this environmental stochasticity can cause transitions to new ecological states, induce ecotone stability, or influence recovery from disturbance (Ridolfi et al. 2011). In community models, environmental stochasticity can slow biome transitions via fluctuation-dependent mechanisms of species coexistence, for example, if species' unique responses to climate reduce the likelihood of competitive take-overs (Angert et al. 2009, Chesson 2000). As climate variance increases, climate differences between consecutive years become more dramatic. This likely affects the role of <u>antecedent effects</u>, in which current biological responses depend on their responses to past perturbations (Ogle et al. 2015). For example, current year primary production can be lower because the prior year was drier than average (Reichmann et al. 2013). Antecedent effects may be particularly important at ecotones, where ecosystems can rapidly expand or contract with extreme climate events (Zimmermann et al. 2009). **Proposed research will compare the strength and drivers of climate-driven antecedent effects among multiple dryland biomes for the first time.** 

### **Research Questions**

Empirical understanding of the effects of climate variance has lagged behind theory because natural climate variability occurs over temporal scales that exceed most ecological studies. A critical unanswered question is whether ecological responses to realistic climates are sufficiently nonlinear to cause large impacts of variance. Experimental tests of this question require long-term funding. Thus, progress depends fundamentally on long-term support by programs such as NSF-LTER.

The new SEV LTER program seeks to understand how and why drylands respond to the interactive effects of climate mean and variance. We will combine long term data, new and existing experiments, and models to characterize the underlying traits and patterns of diversity that explain why dryland biomes vary in ecosystem processes, responsiveness to climate and disturbance, and susceptibility to state transitions. We will link responses across trophic levels to understand patterns and controls on consumer population dynamics. The first six years of our multi-decadal plan will focus on five research questions:

- 1. How do climate variance and long-run mean drive biome transitions?
- 2. Why are some biomes and ecotones more sensitive to climate mean and variance than others?
- 3. How will changes in climate variance and mean affect biome-specific biogeochemical processes and alter biophysical feedbacks?
- 4. How do climate-driven changes in resource landscapes affect consumer dynamics?
- 5. How do disturbances alter climate sensitivity functions or antecedent effects?

With >25 years of long-term data and experimental infrastructure in five dryland ecosystems (Table 1), we are uniquely positioned to address these questions. In the following Domain section, we show how our questions emerge from our long-term data. We then use our Conceptual Framework to integrate understanding of ecological responses over scales of space, time, and levels of biological organization.

#### **Domain of the Sevilleta LTER**

#### Overview.

The Sevilleta National Wildlife Refuge (Socorro, NM) includes five ecosystems that **represent ~80 million ha of the Southwestern US** (Table 1). With the only extensive dry grasslands and dry woodlands in the LTER network, SEV would continue to be a vital

node in cross-site syntheses (>40

Table 1. Geographical representation and current vs. future foundation species of five SEV ecosystems.

SEV Ecosystems	Million ha SW-US	Current Foundation Species	Future Foundation Species
Depart abrubland	20	Crassets bush	Crassets bush
Desert shrublahu	20	Creosole bush	Creosole bush
Desert grassland	25	Black grama	Creosote bush
Great Plains grassland		Blue grama	Black grama
Juniper savanna	6	Juniper	Blue grama
Piñon-juniper woodland	18	Piñon pine	Juniper

pubs. since 2004, cited ~3600 times). SEV biomes collectively support relatively high species richness but are governed by a few foundation species (Table 1), making research tractable. The gradient of SEV ecotones enables robust tests of how climate change will de/accelerate biome transitions, while other dry LTER sites focus on alternative drivers (urbanization, livestock grazing, invasion). For example, our new emphasis on temporal heterogeneity complements work at Jornada LTER on how large-scale transport vectors (e.g., wind) interact with fine-scale spatial heterogeneity (Okin et al. 2015, Peters et al. 2015).

SEV climate. Water is the most vital resource in drylands (Noy-Meir 1973) and shows high temporal variability at local and regional scales (Gutzler & Robbins 2011, Notaro et al. 2010). SEV precipitation is weakly bimodal. Soil moisture accumulates in winter, particularly at higher elevations where snowfall is significant. Warm, dry conditions in late spring create a pulse of snowmelt moisture at high elevation, while severely depleting soil moisture at low elevation. Then, from July through September, the North American Monsoon drives localized convective storms that contribute ~60% of mean annual precipitation. Long-term minimum precipitation is <4mm every month, and precipitation reconstructions using Sevilleta tree-ring record reveal a history of severe drought every 60–70 years since the 17th century (Milne et al. 2003, Parks et al. 2002). Climate models predict higher winter and summer annual temperature, more frequent and intense El Niño events (Power et al. 2013), declines in winter/spring precipitation and more variable monsoon rainfall (Gutzler & Robbins 2011).

Dryland water availability is determined not only by precipitation inputs but also by the strong influence of temperature on evaporative demand (Diffenbaugh et al. 2015, Williams et al. 2013). To account for temperature-driven water deficit, we rely on the Standardized Precipitation Evapotranspiration Index (*SPEI*) (Vicente-Serrano et al. 2010). More negative *SPEI* values signify drier and hotter conditions. *SPEI* thus influences the amount and duration of soil moisture. Since 1989, mean *SPEI* has declined at SEV, while variance in *SPEI* has increased (Fig. 4), a scenario of dual change in climate mean and variance (Fig. 1). Climate warming affects trends in long-run mean *SPEI* (McCabe & Wolock 2015), while altered precipitation amplifies *SPEI* variance.



Fig. 4. Temporal change in mean and *CV* of Standardized Precipitation Evapotranspiration Index (*SPEI*) for a 6-month integration (Apr-Sep) period from SEV meteorological data.

SEV biomes. The diversity of SEV biomes (Table 1) gives us the unique ability to test hypotheses for a range of representative drylands in the SW-S that differ in plant functional types, net ecosystem production (NEP), gross primary production (GPP), ecosystem respiration ( $R_E$ ), soil organic matter, nitrogen (N) availability, and disturbance regimes (Fig. 5, Anderson-Teixeira et al. 2011). From our 10 year record of carbon fluxes, we also know SEV biomes differ in inter- and intraannual variability in both GPP and  $R_E$ , in their sensitivity to *SPEI*, and in the timing of precipitation inputs (Fig. 5-6). We estimate the



Fig. 5. SEV flux tower data. Yearly mean C flux (colored line) with variation over 10 years (gray lines). GPP=negative, Respiration=positive. Mean annual NEP  $\pm$ SE in g C y<sup>-1</sup> in left corner.

collective carbon sink strength of these biomes in NM alone is -11.0  $\pm$  3.7 Tg C/yr with a range from -24 (sink) to 6 (source). Land surface models are notoriously bad at representing dryland biomes, largely due to a poor understanding of biome-specific mechanisms that regulate ecosystem processes, including sensitivity to climate (Ahlstrom et al. 2015). Our proposed research will reduce uncertainties in these important dryland biomes through a new mechanistic focus on the traits that drive biome-specific patterns in carbon uptake and release, and their sensitivities to climate and disturbance.

**Evidence for the Importance of Climate Variance.** Stability of grass-shrub transitions. SEV sits at the northern boundary of Chihuahuan Desert shrubland, where the foundation species changes from creosote bush (*Larrea tridentata*) to the desert grassland dominant, black grama grass (*Bouteloua eriopoda*). Over the past 150 years, shrublands have expanded (Grover & Musick 1990), displacing desert grasslands in a manner similar to woody encroachment occurring globally (Archer et al. 1995, D'Odorico et al. 2012, Eldridge et al. 2011). Curiously, the SEV grass-shrub ecotone has been stable since 2001 (Moreno-de las Heras et al. 2015). Our long-term data



show that shrubland exhibits relatively low inter-annual variation in primary production (Fig. 2), consistent with a climate sensitivity function that



predicts low responsiveness to climate variance (linear, Fig. 7A; quadratic: *P*=0.18). In contrast, desert grassland should benefit from higher precipitation variance under dry conditions (convex at low *SPEI*, Fig. 7B), potentially enabling recent resistance to encroachment. **We will assess how and why (Q1, 2)** increased variance in *SPEI* under higher aridity could explain recent stability of this ecotone.

Grassland transitions. SEV also spans the ecotone between black grama-dominated, Chihuahuan Desert grassland and blue grama (*B. gracilis*)-dominated Great Plains grassland. While black grama has doubled in abundance over the past 20 years, blue grama has declined (Collins & Xia 2015). This pattern seems enigmatic





because black grama is a weaker competitor, less responsive to individual rain pulses, and more sensitive to disturbance than blue grama (Baez et al. 2013, Peters & Yao 2012). Yet, climate sensitivity functions predict that more variable *SPEI* should benefit desert grassland, which is convex at low *SPEI* (Fig. 7B) but be costly to Great Plains grassland, which is concave at low *SPEI* (Fig. 7C). We will determine if and why (Q1, 2) higher variance in *SPEI* under higher aridity explains conversions from Great Plains to Desert grassland.

*Woodland-savanna transitions.* SEV research shows nonlinearity in climate sensitivity at another critical dryland transition: piñon-juniper woodland to juniper savanna. Severe drought triggered rapid tree mortality across the SW-US in 2001–02 (Breshears et al. 2005). SEV woodlands suffered similar mortality following a drought in 2011–2013 (Fig. 8). Piñon-juniper woodlands show high sensitivity of GPP and R<sub>E</sub> to *SPEI* (Fig. 6), as well as strong antecedent effects of prior year *SPEI* (see also Peltier et al. 2016). Across the SW-US, droughtinduced mortality is much higher for piñon pine (*Pinus edulis*) than for juniper (*Juniperus monosperma*) (Fig. 8) due to key differences in their drought tolerance traits



Fig. 8. Relative sensitivity of piñon pine *vs.* juniper to mortality under drought. Negative *SPEI* values (right y-axis) represent hot, dry conditions.

(Plaut et al. 2013), amplified by bark-beetle dynamics (Gaylord et al. 2013). However, loss of piñon pine could indirectly impact juniper, particularly during drought. Our large-scale girdling experiment to simulate piñon mortality (~1600 trees) showed that juniper does not rebound from competitive release as anticipated, but instead declines (Morrillas et al. 2016). Pilot data suggest that piñon may play a key role in maintaining water availability for juniper by reducing near-ground solar radiation and soil evaporation rates (Royer et al. 2010, Royer et al. 2011) and by connecting deep and shallow soil water sources through hydraulic distribution (Morrillas et al. 2016). A transition to juniper savanna, or to a novel grass-dominated ecosystem, may be in progress across the region, with potentially large consequences for both climate sensitivity and C sequestration (Fig. 5-6). We will test if and why (Q2, 5) piñon mortality affects woodland sensitivity to climate and whether accelerated transitions result not only from a drier climate but also a more variable one (Q1).

*Microbial dynamics at dryland ecotones.* Soil microbes play pivotal roles in dryland ecosystems (Belnap & Lange 2003). First, root-associated fungi can affect plant resistance to stress, C and N cycles (Mohan et al. 2014, Porras-Alfaro & Bayman 2011), and competitive outcomes between foundation plants (Chung & Rudgers 2016). Yet, we lack the data to predict long-term microbial responses to climate (Classen et al. 2015, Kivlin et al. 2013) or their dynamics at most dryland ecotones (Barba et al. 2016). Our data, and



Fig. 9. Biocrust disturbance affected biocrust chlorophyll (top) more strongly in grassland than shrubland. Grassland cover was also more sensitive to biocrust disturbance than shrubland cover. n=10 plots (6mX6m) per biome. Means  $\pm$  s.e.

those of others (Karst et al. 2014), suggest these responses could be large; e.g., soil microbial activity responded strongly to piñon mortality (Warnock et al. 2016), and woodland droughts altered the composition of ectomycorrhizal fungal communities (L. Taylor, unpubl. data, Gehring et al. 2014). Second, soil biocrusts can reduce dust emission, alter water infiltration, and fix atmospheric N, an important resource in desert soils (Belnap 2006, Pointing & Belnap 2012, Pointing & Belnap 2014). We showed that biocrusts form biogeochemical bridges to plants, potentially buffering both partners against climatic stress and tightly coupling their resource dynamics (Collins et al. 2008, Green et al. 2008). SEV biomes span a geographically widespread microbial ecotone, where the dominant biocrust cyanobacterium shifts from the hot-adapted species complex *Microcoleus steenstrupii* to cool-adapted *M. vaginatus* (Garcia-Pichel et al. 2013). SEV biomes differ in the functional importance of biocrusts (Fig. 9). In desert grassland, biocrust reduction caused a 20% decline in plant cover (Fig. 9); a 30% decline in black grama strongly contributed to altered plant composition (perMANOVA, *P*=0.007). Yet, in shrubland, disruption of biocrusts had no significant effect on cover (Fig. 9) or on black grama (*P*=0.44). We will determine how climate variance and mean affect microbe-mediated biogeochemical processes (Q3) and whether disturbance of biocrust alters climate sensitivities of plants or processes (Q5).

*Biophysical feedbacks at dryland biome transitions.* Biophysical feedbacks result when foundation species alter the abiotic environment in self-promoting or self-limiting ways (D'Odorico et al. 2013). For example, at SEV grass-shrub ecotones, shrubs contribute to warmer and drier surface soils by altering outgoing longwave radiation, thereby benefitting themselves over grasses (He et al. 2015, He et al. 2010). If unaccounted for, such feedbacks could produce large uncertainties in the predicted trajectories of biome transitions (Jiang et al. 2016, Singer et al. 2016). Our long-term data suggest that feedbacks occur in all SEV biomes, but only those in shrubland are well-documented. In woodlands, piñon mortality may increase rates of snow sublimation and soil evaporation and reduce hydraulic redistribution, leaving soils both hotter and drier and potentially accelerating transition to a new state (Morrillas et al. 2016). In desert grasslands, hot-adapted biocrust cyanobacteria make the sunscreen scytonemin for UV protection, but in so doing, darken and warm soils (Couradeau et al. 2016), possibly exacerbating water limitation. Positive interactions between grasses and biocrusts (Fig. 9) could retain soil moisture and nutrients within a fungal feedback loop (Collins et al. 2008). We will determine how biophysical feedbacks respond to climate mean and variance to affect individual ecosystems and their ecotones (Q3).

*Consumer dynamics at dryland ecotones.* How do consumers respond to and interact with dryland biome transitions? SEV's consumer community is dominated by small mammals and grasshoppers. The refuge has been fenced from livestock since 1973 and has low native ungulate abundance. Consumer abundance tracks primary production and the biomass of nutritious  $C_3$  plants, a resource that is easily traced via carbon isotope analysis (Warne et al. 2010). In fact, our long-term small mammal exclusion showed no top-down effects on plants (Baez et al. 2006). In grasslands, small mammals track summer monsoon  $C_3$  production, but in shrublands they are more responsive to spring  $C_3$  biomass (Fig. 10, top panels). Body condition data also support the importance of  $C_3$  resources for small mammals. For example, silky pocket mice (*Perognathus flavus*) that consume a diet dominated by  $C_3$  resources have



Fig. 10. Relationships between small mammal (top plots) and grasshopper (bottom plots) abundance and C<sub>3</sub> plant production (excluding inedible creosote bush) across SEV biomes. GLMMs with 95% CI bands.



Fig. 11. Percent body fat of silky pocket mice that specialize on  $C_3$  plants vs. consume a mixed diet.

higher percent body fat than generalist individuals that consume a mixed diet of  $C_3$  and  $C_4$  plants (Fig. 11). In woodlands, our 19-year data set on mast seed production by ~900  $C_3$  trees – piñon, juniper, and oak (*Quercus turbinella*) – drives saturating increases in small mammals during the following year (see also, Bombaci & Pejchar 2016). SEV grasshoppers were 1.9–6.8X more responsive to  $C_3$  production (Fig. 10, bottom panels) than to total primary production (*data not shown*), and concave nonlinearities for grassland orthopterans indicate that higher variance in  $C_3$ resources will be costly.  $C_3$  biomass has recently declined in all SEV biomes (Fig. 12). We predict lower  $C_3$  plant biomass in future climates because  $C_3$  climate sensitivity functions flip from convex to concave as *SPEI* declines (as in Fig. 3C). Thus, as climate warms, more variable precipitation should further reduce  $C_3$  biomass (Collins et al. in revision, Mulhouse et al. in review). Climate-induced shifts in vegetation will affect

the foraging decisions that determine consumer survival, body condition, and reproduction. Yet, the physiological mechanisms that underlie consumer dynamics over these changing resource landscapes are not resolved for any dryland. This limits predictive power and generalization to other ecosystems. We will evaluate these mechanisms to improve forecasts of consumer dynamics at biome transitions (Q4) and advance general theory on foraging ecology in variable, resource-limited environments.



Fig. 12. Temporal declines in  $C_3$  biomass in SEV biomes. These long-term patterns correspond with climate sensitivity functions that indicate costs of variance under drought conditions (low *SPEI*).

Summary. Altogether, the SEV LTER legacy, and in particular, our 28-year record of high quality, long-term data, provides a rich foundation for understanding individual, population, community, and ecosystem dynamics across a range of dryland biomes. Since 1988, we have produced 210 data packages that are publicly available on the SEV website, trained >150 undergraduates, and mentored 59 MS and PhD theses. We secured \$46 million in companion grants, \$9.1 million in the last 6 years alone. Our SEV publications total 687 and counting and have been collectively cited >41,000 times. *This legacy allows us to push the frontiers of science by developing and testing a new conceptual framework that will explain, for the first time, whether and how change in the mean and variance of climate alters the dynamics of dryland ecosystems and their ecotones, and why some populations, communities, and ecosystems are more sensitive to climate variability than others.* 

#### **SEV Conceptual Framework**

Our conceptual framework is built around the overarching question: **How do changes in climate mean and variance independently and interactively affect the dynamics of dryland ecosystems and the transitions among them?** We propose a multi-decadal vision for the SEV LTER that will integrate understanding of dryland dynamics across scales of space, time, and biological organization through explicit predictions from different sub-disciplines of ecology. This framework allows us to not only explain why drylands have changed historically, but also predict how their structure and function will change in the coming decades. We build on work that has eliminated earlier hypotheses on the drivers of biome transitions (e.g., El Niño events, pulse dynamics). Pre-proposal reviews (3E, 1G) noted that our study of multiple biomes is a powerful tool for developing general theory. While reviewers praised our clear central focus derived from theory, project integration, and seamless extension from populations to ecosystems, one reviewer challenged us to further highlight aspects that are novel or cutting edge. We do so below.

In our Conceptual Framework (Fig. 13), boxes graphically illustrate key predictions from ecological theory at different spatial, temporal, and biological scales. We begin with Biome Transitions (Box A). Then, we illustrate how processes that originate with climate drivers affecting individual organisms (Box B) determine changes in the traits of populations and communities (Box C) that alter climate sensitivity functions (Box D) to either accelerate or inhibit biome transitions. Finally, we consider how dryland disturbances (Box E) may modulate the sensitivity of ecological processes to climate.

#### **Biome Transitions.**

We predict, and our long-term observational data support, an important role for the *interactive effects* of climate mean and variance in driving biome transitions. Interactive effects may accelerate transitions (**Box A**) causing species take-overs and shifting ecotone locations in space. Alternatively, interactions could inhibit transitions, or even expand ecotones, by promoting competitive coexistence via fluctuation-dependent mechanisms (Chesson et al. 2004, D'Odorico et al. 2008). Prior work in drylands and other biomes has combined observations and models to predict transition dynamics. For instance, eco-hydrological models are particularly well-developed to account for stochasticity in soil moisture and, in some cases, inter-annual variance in precipitation (e.g., Caylor et al. 2009, Feng et al. 2015, Porporato et al. 2004, Xu et al. 2015b). While

Fig. 13. SEV Conceptual Framework: Predicted responses to climate scenarios of higher mean drought (orange) or higher variance in drought (blue); gray lines show the expected ambient pattern.

How do changes in climate mean and variance independently and interactively affect the dynamics of dryland ecosystems and transitions among them?



these approaches vield important insight at the landscape scale (e.g., tree-grass ecotones), they do not build from lower level processes: traits and evolutionary change, diversity and its maintenance, or species interactions and demography. New modeling approaches are needed to integrate biological mechanisms, such as dispersal, demography, and interactions among foundation plants. Process-based models can improve predictions into no-analog futures. We aim to resolve the causes and consequences of biome transitions, by linking the evolution of foundation species (Box B) with population, community, and ecosystem dynamics (Box C-E).

# Traits and Diversity: Individuals to Communities.

Because traits reflect the physiological mechanisms of responses to the environment, they transcend species identities and enable the generalization of predictions to other ecosystems (Diaz et al. 2016). Traits also link evolutionary change with ecosystem processes (Bardgett et al. 2014). Along a 'resource economic' spectrum (Reich 2014, Weemstra et al. 2016, Wright et al. 2004), conservative traits protect species against stress and drive slow processes. For plants, these include e.g., high values of water use efficiency or leaf [C]:[N] ratios. Conservative traits typically trade-off against acquisitive traits (Silvertown et al. 2015), which enable rapid resource acquisition and fast turnover (e.g., fast growth, low leaf [C]:[N]). Animals have similar spectra, with resource-caching behavior and large body size at the conservative end (Scherer et al. 2016).

*Trait change: Individual organisms* (**Box B**). A change in mean climate will have different evolutionary consequences than a change in variance. For example, a change from present (gray line) toward increased *mean* drought (orange line) should select more water-conserving traits. In contrast, higher climate *variance* (blue curve) may cause disruptive selection, favoring highly conservative and acquisitive tails of the trait spectrum. Such predictions are not new, but are fundamental to a mechanistic understanding of how variance in climate will alter trait distributions.

*Trait change: Populations and communities* (**Box C**). Populations respond to climate change through acclimation and/or evolution, shifting intraspecific trait distributions along the conservative-acquisitive axis. Climate-driven change in population traits has landscape scale consequences when it alters community trait distributions. Community trait distributions result from species traits weighted by species relative abundances (Shipley 2010), abundances that SEV has monitored for 17–28 years. First, change in the climate mean should shift traits toward conservative values (reviewed by Ackerly 2003,



Fig. 14. Predicted trait variance. extr

Anderson 2016, Gienapp et al. 2008, Hoffmann & Sgro 2011). Second, theory predicts that trait variance should peak at intermediate climate variance (Fig. 14, Net Effect), due to opposing forces. Climate variance should *promote variance* in community and population trait distributions by maintaining species diversity (Chesson 2000), genetic diversity (Bell 2010), and phenotypic plasticity (Chevin et al. 2010) through fluctuation-dependent mechanisms. However, when

extreme climates cause extinctions or evolutionary tipping points via

environmental and demographic stochasticity (Adler & Drake 2008, Botero et al. 2015), very high climate variance should *reduce trait variance*, causing an intermediate peak. This hypothesized peak has received few direct tests, despite studies of individual extreme events (Gutschick & BassiriRad 2003, Vazquez et al. 2016). In general, mean traits are better resolved than trait variance (Moran et al. 2016, Violle et al. 2012). However, trait variance is important because this variance, and its underlying genotypic or species diversity, can buffer against future climate stress and disturbance (e.g., Hart et al. 2016, Isbell et al. 2015). Furthermore, because traits, particularly those of foundation species, drive many ecosystem processes (Bardgett et al. 2014), a trait-based approach can help to refine predictions of ecosystem change (Luo et al. 1994).

Mechanisms of Climate Sensitivity: Populations to Ecosystems.

We predict that climate variance and mean will affect dryland population, community, and ecosystem dynamics through <u>climate sensitivity functions</u> and <u>antecedent effects</u> (**Box D**). New theory will come from determining whether and when the mean and variance of specific traits correlate with the shape of sensitivity functions or size of antecedent effects, enabling generalization to other dryland ecosystems.

*Population dynamics*. Conservative traits should cause lower sensitivity to climate variance. In contrast, acquisitive traits may amplify the benefits of climate variance, by enabling species to respond quickly when resources are available (convex shape, Box D). Pilot SEV data support this idea. Plant species with more conservative traits had less temporal fluctuation in biomass (smaller *CV* over 12 years), including species with deeper roots, shorter height, and higher leaf [C]:[N] ratio (Fig. 15).

*Ecosystem processes.* In communities dominated by species with resource-conserving traits, ecosystem processes (i.e., carbon, water and nitrogen dynamics) should be less sensitive to climate change than in communities dominated by acquisitive traits. For example, resource-



Fig. 15. Plant species with more conservative traits showed less temporal fluctuation in biomass (*CV*). Each point is a phylogenetically independent contrast (*PIC*) between clades; *PIC*s can be negative even when the original variable cannot. conserving desert shrubland, dominated by slow-growing and deep-rooted creosote bush, should have weaker climate sensitivity than more resource-acquisitive grasslands with faster growth and quicker turnover of shallow roots (see Fig. 7). Not only will the mean values of traits be important to predicting responses at larger scales, but trait variance may also be critical (Jump et al. 2009). Wide variance in traits, like high biodiversity, could buffer systems against climate fluctuation (Isbell et al. 2015), a hypothesis not yet tested in drylands, despite their high variability (Fig. 2). Although climate sensitivity functions have gained traction in population ecology (Bozinovic et al. 2011, Ehrlen et al. 2016, Vazquez et al. 2016), few community or ecosystem-scale studies have looked for such nonlinearities (but see, Forzieri et al. 2014, Haverd et al. 2016, Hsu & Adler 2014a). This means we lack fundamental knowledge to predict responses to climate variance.

# Ecosystem Processes and Biophysical Feedbacks.



Climate-induced shifts in the trait distributions of dominant producers should have direct consequences for ecosystem and biogeochemical processes (Cornwell et al. 2008, DeMarco et al. 2014, Hobbie 2015, Holzwarth et al. 2015). Although climate-driven changes in traits could simply shift the rate of an ecosystem process (e.g. NEE,  $R_E$ ) to a different value (Fig. 16, orange & blue points), climate change could also profoundly alter the relationship between a trait and process (Fig. 16, dashed line). In addition, changes in climate mean and variance could alter the strength of biophysical feedbacks in ways that

accelerate or inhibit biome transitions, dramatically altering predictions (Jiang et al. 2016, Singer et al. 2016). It remains unclear whether or when such changes will occur in drylands experiencing greater inter-annual climate variance. Plant species removals provide a powerful tool to assess feedbacks by comparing processes in the presence versus absence of a foundation species (e.g., Suding et al. 2008).

# Disturbances.

Disturbances, both chronic and episodic, could amplify or buffer the sensitivity of ecological responses to climate (**Box E**) (Eskelinen & Harrison 2015, Smith et al. 2009). Prior SEV research suggests several possibilities. Nitrogen-deposition could lessen the costs of climate variance by relaxing nutrient limitation of productivity during wet years, thereby reducing concavity of the climate sensitivity function. In SEV grasslands, fertilization increased productivity only during wet years, when water limitation was relieved (Ladwig et al. 2012). Likewise, experimental warming increased C<sub>3</sub> forb cover, but only after a severe fire (Collins et al. in revision). Biophysical feedbacks at grass-shrub ecotones slowed after fire reduced spatial heterogeneity in resources (Ravi et al. 2009). Woodlands were more sensitive to drought following the disturbance caused by severe piñon mortality (Morrillas et al. 2016), and woodland N-additions reduced ecomycorrhizal fungi and caused piñon to die in the 2001-2 drought (Allen et al. 2010). How does disturbance modify non-linear climate sensitivity and antecedent effects? This question is unresolved because direct tests require long-term experiments over naturally variable climates or joint manipulation of disturbance and climate variance. However, ignoring key disturbances in drylands could gravely misrepresent their futures.

### Hypotheses

Our overarching research goal is to examine: **How changes in climate mean and variance independently and interactively affect the dynamics of dryland ecosystems and transitions among them?** Here, we present hypotheses (in *italics*) for the five questions we previously introduced and explain how we will test them. Our general approach combines long-term datasets and experiments with theory and models from different sub-disciplines of ecology. Roman numerals map to specific methods provided in the Research Activities section. Coverage of LTER core areas appears in Table 2.

#### 1. How do climate variance and long-run mean drive biome transitions?

We hypothesize that interactions between climate mean and variance will be more important in shifting ecotone boundaries than either the mean or variance in climate alone. Climate change will either accelerate transition by causing competitive take-overs or inhibit transition by promoting competitive coexistence (Fig. 13, Box A), depending on the lower level drivers at each ecotone (Box B-E).

To test these hypotheses, we plan a new cross-biome experiment that factorially alters the mean and variance of soil moisture for the first time (**I. Mean-Variance experiment**), mimicking anticipated change in dryland *SPEI*. Our long-term field data and new remote sensing (**II. LTER Core Observational Data**) will not only record historical and future biome transitions but also allow us to determine climate sensitivity functions and antecedent effects for foundation plant species and scale up to the SW-US region. We will merge Mean-Variance results with data on interactions among foundation species (**IV. Foundation Species Removals**) and long-term observations using a new model (**VI. WAVE**). To forecast biome transitions under climate change, WAVE combines demographic, competitive, and dispersal dynamics of foundation plant species using dispersal kernels and integro-difference equations for population growth.

# 2. Why are some biomes and ecotones more sensitive to climate mean and variance than others?

We hypothesize that populations/communities/ecosystems dominated by resource-conserving traits will be less sensitive to change in climate (Box D) than those dominated by acquisitive traits. Higher trait variance or diversity should buffer against climate variability, compared to systems with lower trait variance. We do not expect trait distributions to be static. Long-term change in both the mean and variance of climate should push the trait mean toward resource-conservative strategies (Box B-C), and trait variance should peak at intermediate climate variance (Fig. 14). We will track trait and evolutionary change with the first SEV Trait Database and a new Evolutionary Monitoring Program (III. Traits, Diversity, and Evolutionary Monitoring). Using long-term abundance data and experimental results, we will monitor change in the population trait distributions of each foundation species and in the community trait distributions of each biome. We will then generate new theory by evaluating whether and how these trait distributions (Box C) control the shape of climate sensitivity functions or size of antecedent effects (Box D), which we obtain from ongoing LTER Core Observational Data at population-to-ecosystem levels (e.g., foundation species, ANPP, NEE). We will also test the degree to which nonlinearities and antecedent effects derived from observational data predict the effect sizes of responses to direct manipulations of climate in our Mean-Variance experiment. To project dynamics into the future and explore parameter space beyond what we can manipulate, we will develop the first dryland version of the Terrestrial ECOsystem Model (VI. TECO). A widely used model that simulates biophysical and biogeochemical processes, TECO will assimilate SEV data to forecast changes in ecosystem function under alternative climate scenarios. We will build a new front-end to TECO that links traits to ecosystem processes. By varying trait distributions in TECO simulations, we can evaluate how trait change alters ecosystem sensitivity to climate over long time periods.

# 3. How will changes in climate variance and mean affect biome-specific biogeochemical processes and alter biophysical feedbacks?

We predict that climate change will alter biophysical and biogeochemical processes by shifting trait distributions within biomes (Box C) or by fundamentally changing relationships between traits and process rates (Fig. 16). Climate change may intensify biophysical feedbacks for foundation species that benefit from climate variance (convex nonlinearity) or weaken feedbacks for species that experience costs of variance (concave nonlinearity, Box D). Such altered feedbacks could accelerate or inhibit biome transitions (Box A). In each SEV biome, we will use LTER Core Observational Data on soil moisture, temperature, and ecosystem fluxes to describe biome-specific processes and detect signatures of feedback, such as strong correlations with foundation plant abundance. We will add a new, cross-biome dataset of [C]:[N] ratios to alert us to coarse-scale changes in the stoichiometric landscape, which we will then investigate more closely using short-term measurements of process rates. We will test if and how relationships between traits and processes shift with climate in our Mean-Variance experiment and with disturbance in ongoing projects (V. Disturbances). To assess feedback experimentally, we will compare biogeochemical and physical properties in the presence versus absence of foundation species (IV. Foundation Species Removals). Finally, we will harness the TECO model to forecast ecosystem responses under scenarios of climate-altered feedbacks.

# 4. How do climate-driven changes in dryland resource landscapes affect consumer dynamics?

Consumers can respond to the direct influences of climate as well as indirect effects via altered resource landscapes. We hypothesize that consumers with resource-conservative traits will be less sensitive to

climate change (Box D) than those with more acquisitive traits. Species with acquisitive traits should benefit more from climate variance than those with conservative traits. High trait variance and diversity will buffer populations experiencing high climate variability. We will use LTER Core Observational Data to evaluate the relative importance of direct versus indirect effects of climate on SEV's key consumers: small mammals and grasshoppers. Our long-term data permit the estimation of species-specific climate sensitivity functions and the size of antecedent effects. However, mechanistic understanding must incorporate foraging decisions in temporally stochastic resource landscapes, decisions that are influenced by consumer traits, food abundance and quality, existing reserves, and risk of predation. Thus, we will merge new measures of consumer traits (III. Traits) with a novel Stochastic Dynamic Programming model (VI. SDP) to shed light on mechanisms affecting consumer fitness in variable climates. Results from WAVE and TECO will allow forecasts of consumer dynamics in climate-altered resource landscapes.

# 5. How do disturbances alter climate sensitivity functions or antecedent effects?

Abiotic and biotic disturbances can either buffer or amplify ecological responses to climate change (Box *E*) by altering climate sensitivity functions and antecedent effects. For example, disturbances that rapidly disrupt foundation species may amplify sensitivity to climate by increasing concavity of the climate sensitivity function. We will re-envision long-term experiments and disturbance monitoring efforts to newly test whether disturbances modulate ecological responses to natural climate variability (**V. Disturbances**). For example, long-term fertilization and new N-additions to our **Mean-Variance experiment** will test whether chronic N deposition could alleviate secondary resource limitation and lessen sensitivity to climate variance by reducing concavity in the sensitivity function. For each disturbance dataset, we will use **LTER Core Observational Data** over SEV's naturally variable climate to compare climate sensitivity functions will be integrated into **WAVE**, **TECO**, and **SDP** to predict long-term impacts of the disturbances most relevant to each biome: mass tree mortality in woodlands, extreme drought in grasslands, and natural and prescribed fires. We will also expand biocrust disturbance experiments into all SEV biomes. For example, we predict that biocrust presence could dampen sensitivity to climate in some biomes by benefitting foundation plant species (Fig. 9).

#### **Research Activities**

To advance a process-based predictive understanding of how climate affects populations, communities, ecosystems, and their ecotones, we propose an integrated research program with new experiments, observations, and modeling. In particular, our long-term observations, along with data from prior and proposed experiments, will be assimilated into three models to predict responses to climate variability for (1) biome transitions (WAVE), (2) ecosystem processes (TECO), and (3) consumer dynamics (SDP). Below, we address reviewer suggestions to fully explain how data collection and modeling approaches are appropriate to our program (see also Table 4).

# (I.) Mean-Variance Experiment —

We propose a novel experiment, replicated in five SEV biomes, to alter the mean and variance of soil moisture, as the key manifestation of *SPEI*. Because we focus on inter-annual variability, this experiment would not be possible without long-term funding. Recent work shows precipitation variance manipulations are feasible, and in just 6 years increased precipitation variability reduced black grama by 80% but boosted the cover of mesquite shrubs by 67% at a Jornada site (Gherardi & Sala 2015a). We will add **three novel elements** by (1) determining interactive effects with a factorial design that crosses reduced mean with increased variance, (2) studying five dryland biomes to compare their susceptibility to transition, and (3) adding stochasticity to our manipulations to permit the antecedent effects that occur under natural climate variability.

#### Experimental Design.

To increase **variance** in soil moisture ( $\theta$ ) stochastically, without changing the mean, we will pair plots and amplify their precipitation regimes (Fig. 17). Specifically, every water year, plots within a pair will be randomly assigned to either a 50% decrease or 50% increase in precipitation. Gheradi and Sala (2015a) showed that a 50% change produced a 66% increase in the coefficient of variation (*CV*) of precipitation,

	Ambient Mean mock shelter	Reduced Mean -25% preciptation	
Ambient Variance mock shelter	n=5	n=5	
Increased Variance ±50% precipitation	n=10 (5 pairs)	n=10 (5 pairs)	

Fig. 17. Mean–Variance experiment design.

matching our projected regional climate extremes. However, because they were not testing for antecedent effects, they applied regular alternation between high and low rainfall years, which reduced stochasticity. Our proposed treatment will create stochasticity through random assignments. To reduce the long-run **mean** soil moisture ( $\theta$ ), we will intercept 25% of precipitation, a moderate forcing within range of likely futures (Seager et al. 2013). We will cover each 5mX5m plot with roof panels that intercept precipitation year-round

(Yahdjian and Sala 2002). Control plots will receive similar shelters but with panels that allow precipitation through. Plots receiving both reduced mean and increased variance will randomly alternate between 75% less net precipitation (-25% for mean - 50% for variance) or 25% more (-25% for mean + 50% for variance). Water will be captured from shelters with gutters, stored in tanks, then delivered to the paired plots via solar-powered pumps (Gherardi & Sala 2013). Replication is uneven to account for higher variability among plots in the increased variance treatment (Fig. 17). All 30 plots per biome will be hydrologically isolated via flashing and co-located with existing meteorological stations. Plots in woodlands will be located near, but not including, adult trees.

*Proof of Concept.* Simulations of historical SEV met data (Fig. 18) show that 25% rainfall reductions will reduce *SPEI* by ~19% while 50% deviations will increase the *CV* of *SPEI* by ~53%, <u>without altering its</u> mean under feasible replication (22 plots simulated per biome).

#### Response Variables and Analysis.

Recruitment: Seed and seedling additions. Each year, we will introduce seeds and seedlings of "Current" and "Future" foundation plant species (Table 1) to determine recruitment and establishment. These additions test whether and at what rate a species introduced at low density is competitively excluded by resident dominants, a key determinant of species coexistence versus take-over (Chesson 2000). Additions will occur in 1mX1m subplots, and new cohorts will be added yearly. Recruits that establish will be removed after 3 years, freeing subplots for later additions, and focusing on early establishment processes. Recruitment rates under intra-specific vs. inter-specific



Fig. 18. Mean-Variance simulations of data from SEV met stations. **+Variance** increased *CV* of *SPEI* by 53%.

competition are integral to using our WAVE model (see VI.) to predict how climate affects ecotones. *Other responses.* We will monitor LTER core areas: Above- and belowground production (Ladwig et

al. 2012); plant demography via marked residents; biocrust cover and composition; decomposition of standardized litter (Keuskamp et al. 2013); and plant, biocrust, and rhizospheric soil [C]:[N]. Sensors in 18 plots/biome will track soil moisture and temperature at three depths (12.5, 22.5, 37.5 cm; EC-TM5, Decagon, Pullman, WA) that match depths at our flux towers where we see the strongest biological responses. While we lack budget capacity to add CO<sub>2</sub> sensors, we can accommodate them in the future.

Hypothesis tests - Data analysis. To test (Q1), mean × variance interactions will be more important than mean or variance alone, data will be analyzed with general linear mixed effects models that include the mean and variance treatments and their interaction, as well as the random effect of plot to account for non-independence of repeated observations (R Core Team 2016). Recruitment and establishment data will also be incorporated into the WAVE model (see VI.) to predict the direction and trajectory of biome transitions in response to mean × variance treatments. As we accumulate a time series, we will use stochastic antecedent modeling to detect the presence, size, length, and temporal pattern of antecedent responses to stochastic treatment histories (methods in Ogle et al. 2015). To test (Q2), *if observed nonlinearities in climate sensitivity functions and antecedent effects predict ecological sensitivity climate mean and variance*, we will leverage LTER Core Observational Data over naturally variable climates to determine climate sensitivity functions (as in Fig. 7) and the nature of antecedent effects. We will then evaluate the degree to which effect sizes (e.g., RII, Armas et al. 2004) from our Mean-Variance experiment can be predicted from observed climate sensitivity functions and antecedent effects.

#### (II.) LTER Core Observational Data -

Existing LTER Datasets. SEV's 28 year data legacy has complete coverage of the five LTER core areas

Table. 2. Key SEV LTER datasets. B= Great Plains grassland, C= Desert shrubland, G= Desert grassland, J= Juniper savanna, P= Piñon-juniper woodland. Core = LTER area.

Data set	Core	Dates	Biome
Existing Datasets	·		
Plant composition, ANPP	1	1999/2002-	All
Root biomass, BNPP	1	2005-	BCG
Plant phenology	1	2000-	BCG
Plant demography, masting	1,2	1997/2010-	JP
Tree ring cores	1	1598-	Р
Small mammal abundance	2	1989-	All
Grasshopper abundance	2	1992-	BCG
Bee abundance	2	2001-	BCG
Biocrust chIA, scytonemin	1,2	2013-	CG
Arthropods - Biocrust plots	2	2013-	CG
Flux tower datasets	3,4	2007-	All
Decomposition of litter	3	1990-1999	All
Soil organic matter	3	1989-2014	G
Regional climate	4	1900-	All
Local climate (10 met stns)	4	1988-	All
Rainfall chemistry (20 stns)	4	1989-	All
Soil moisture (20 stns)	4	1989-	All
Soil [C]:[N]	4	2007-	All
Soil available [N]	4	1989-2014	G
Soil [C], NPK	4	1989-	BCG
Fire history	5	1989-	All
Shrub and tree mortality	5	2007-	JP
New Additions			
(I) Mean-Variance experiment	•		
Drope acquired imageny	1	2V vear	A11
Plant composition ANPP	1	2X year	
Seed ( seedling demography	1	1X year	
Boot hismans, BNDD	1		
Root biolilass, BINFF	1	2X year	
	1	1X year	
Phizospheric soil	2	1X year	
Rilizospiteric soli Biogrupt	2	1X year	
CI:INI: Leaf soil biocrust	2		
Soil moisture & temperature	3,4	years. 1,5,0	
	4	36113013	
(II.) LTER Core Datasets	-	Г	1
Biome transitions: Landsat	1	1986-	All
Drone-assisted imagery	1	2X year	All
Biogeochemistry	3,4	see I, IV, V	All
(III.) Trait Database			
Plants	1	vears: 1.6	All
Biocrust & rhizosphere	2	vears: 1.6	All
Grasshoppers	2	vears: 1.6	All
Small mammals	2	vears: 1.6	All
		,,.	
(III.) Evolutionary Monitoring			
Foundation plants (5 spp.)	1	years: 1,6	All
Biocrust & rnizosphere	2	years: 1,6	All
Grasshoppers (11 spp.)	2	years: 1,6	All
Small mammals (6 spp.)	2	years: 1,6	All
(IV.) Foundation Plant Remov	al Distur	bance	
Plant species composition	1	1X year	All
Plant traits	1	years: 1,6	All
[C]:[N]: Leaf, soil, biocrust	3,4	years: 1,3,6	All
Soil moisture & temperature	4	sensors	All
(V.) Biocrust Disturbance			
Plant composition, ANPP	1	2X vear	All
Biocrust: -80C, chIA	2	2X year	All
Rhizosphere soil: -80C	2	2X year	All
Arthropod food web	2	2X year	
[C]:[N]: Leaf soil biocrust	34	vears: 136	
Soil moisture & temperature	4	2X vear	

(Table 2); continued monitoring is essential to all proposed research questions (Q1-5). SEV met stations occur in each biome and ecotone. Twice yearly, we collect plant species biomass estimates in all biomes and experiments (*N*=862 1m<sup>2</sup> quadrats) and counts of 55 grasshopper species (Lightfoot), 31 small mammal species (Newsome), and arthropods in biocrust plots (Rudgers). Once yearly, we collect data on belowground biomass (BNPP, Collins) and demography of >500 individuals of each foundation species (Muldavin, Miller). We also measure soil [C]:[N] yearly, and soil [C]:[P] at 3–5 year intervals.

#### Existing Flux Tower Network. (Litvak)

Our flux towers provide long-term data on ecosystem responses to climate, allowing us to estimate ecosystem climate sensitivities and antecedent effects and scale-up the ecosystem consequences of biome transitions. We will use data from this network to answer Q1, Q3, and Q5, and provide a source for validation of our TECO model. We have continuously measured ecosystem carbon, water, and energy fluxes using open-path tower-based eddy covariance, and associated meteorological variables, in grassland and shrubland biomes since 2007, and in juniper savanna and piñon-juniper woodland since 2008. In 2009, we installed an additional tower in burned grassland following a wildfire and a second woodland tower to quantify the ecosystem consequences of experimental piñon mortality via girdling (DOE BER, DOE-EPSCoR). Flux towers were funded initially by UNM and external grants (NASA, USFS, DOE, NSF) to Litvak; they are now core Ameriflux sites funded by the Ameriflux Management Project at least through 2021 (DOE).

# New Remote Sensing. (Lippitt, Lippitt)

We will use Landsat and Sentinel 2 imagery to track historical and ongoing biome transitions in the greater SEV region, informing (Q1). In addition, we will use hyper-spatial (1-10 cm) resolution images of plots in our Mean-Variance experiment (with shelter roofs removed) to collect a time series of cover data and map fractional cover and biomass (Cunliffe et al. 2016, Zhang et al. 2016). This will allow \_ existing field plots to bridge the gap between plot-based and satellite-based estimates and yields new data for testing climate sensitivities in (Q2). New data will include (1) SEVwide fractional cover/biome type using multiple-end member spectral mixture analysis (MESMA) (Powell et al. 2007) on archived and current LandSat and Sentinel 2 imagery (c. 1986) and (2) tree and shrub demography from hyperspatial resolution airborne color-infrared imagery (already in use for piñon and juniper). Multiple endmember spectral mixture analysis (MESMA: Roberts et al. 1998) will be conducted on LandSat Thematic Mapper (TM) and Sentinal-2 scenes captured between 1984 and 2021 on a 2-3 year interval to estimate changes in the fractional cover of green vegetation, non-photosynthetic vegetation, bare soil, and dominant species for the greater SEV region. TM data have

been successfully used to estimate seasonal and inter-annual variation in greenness at SEV (Pennington & Collins 2007). Linear spectral unmixing (SMA) reliably permits the estimation of fractional land cover within a pixel (Small 2001), allowing remote sensing to adopt the more ecologically appropriate ontology of land cover as a continuously varying property at the spatial scales observed by moderate resolution remote sensing instruments (Strahler et al. 1986). MESMA, an extension of SMA, incorporates myriad cover types (e.g., individual grass and shrub species) for each endmember, permitting more accurate estimates of species dominance (Okin et al. 2001, Painter et al. 1998, Powell et al. 2007). We will use time series of fractional cover change to quantify vegetation change at the landscape scale, map biome transition velocity (i.e., directionality and rate) in the greater SEV region, and, coupled with tower data and model output, to infer the impact of these changes in fractional cover on biophysical variables (e.g., biodiversity, NPP, C storage, soil erosion, microclimate).

#### New Biogeochemistry Data. (Sinsabaugh, Newsome, Vargas)

To track changes in nutrient cycles within each SEV biome and in our Mean-Variance experiment, we will build a new long-term dataset to obtain [C]:[N] ratios of foundation plants, rhizosphere soils, and biocrusts (Fig. 19). These pools are the stoichiometric drivers of N fixation; N mineralization; C and N translocation; microbial growth, respiration, and carbon use efficiency; as well as soil organic matter accumulation

(Moorhead et al. 2016, Sinsabaugh et al. 2013, Sinsabaugh et al. 2016). These data inform (**Q3**) because climate shifts can affect the stoichiometric landscape by altering N deposition (since 1989, Table 2), process windows and rates, and both microbial and plant community composition (Burns et al. 2013). Proposed [C]:[N] data will capitalize on the new UNM Center for Stable Isotopes and alert us to changes in stoichiometry that we can investigate in more detail with short-term measures of process rates, as in our past work (Cregger et al. 2014, Green et al. 2008, Ladwig et al. 2015, Limousin et al. 2015). At minimum, we will collect leaves of each foundation plant, rhizosphere soil, and adjacent biocrust for [C]:[N] in our Mean-Variance experiment (3 tissue types × 5 biomes × 30 plots per year), using control plots to represent each biome. We will link these changes to consumer diets as described next.



*SEV Trait Database: Traits as Predictors.* (Lightfoot, Muscarella, Newsome, Pockman, Whitney, Wolf)

Traits and diversity are key to addressing (Q2), Why are some biomes and ecotones more sensitive to climate mean and variance than others? They are also essential to understanding biophysical feedbacks (Q3) and the climate sensitivities of consumer populations (Q4). Because knowledge of organismal traits is essential to multiple goals in this proposal, we will assemble existing and newly collected data into the first SEV Trait Database. In years 1-3, we will capitalize on SEV data and specimens to compile existing trait data for >100 spp. and >14,000 SEV specimens housed in UNM Museum of Southwestern Biology. We will then initiate a field campaign to fill data gaps. A preliminary list of target traits (Table 3) will be expanded as more research comes to light on generally important predictors of organismal performance. Following established protocols for standardized trait data (e.g., for plants, Perez-Harguindeguy et al. 2013), we will sample at least 10 individuals per species per biome. Additional data will be collected in the Mean-Variance experiment and during ongoing fieldwork to generate robust estimates of intraspecific trait variation, within and across biomes. We will prioritize collection by species' relative abundance.

*Justification for traits.* We focus on traits important to the performance and persistence of primary producers and consumers in arid ecosystems (Table 3). For instance, leaf traits that mediate water balance, tolerance to drought, and herbivory include specific leaf area (Harrison et al. 2015), water



Fig. 19. Desert grassland [C]:[N] ratios show potential fluxes.

Table 3. Focal traits for plant and consumer species. A + (-) sign means that higher (lower) values of the trait signal a more conservative strategy.

#### Plant traits

Specific leaf area (-)
Water use efficiency (+)
Stomatal density/size (-)
Leaf [C]:[N] ratio (+)
Rooting depth (+)
Specific root length (-)
Height (-)
Perenniality/Lifespan (+)
Seed mass (+)
Seed dormancy (+)
Consumer traits
$\delta^{13}$ C value (+)
$\delta^{15}$ N value (-)
Body mass (+)

Litter/clutch size (-)

use efficiency (Angert et al. 2009, Wang et al. 2013), and leaf [C]:[N] ratio (Taylor et al. 1989). Belowground traits are relevant for plant response to precipitation variability and include rooting depth and specific root length (Weemstra et al. 2016). Other plant traits such as height (Fernandez-Going et al. 2012), lifespan, seed mass (Carmona et al. 2015), and dormancy (Salguero-Gómez et al. 2012) affect plant responses to precipitation in drylands (e.g., heavy seeded tend to be favored under drought, Leishman 1999). For consumers, we will use blood plasma (rodents) or whole body (grasshoppers)  $\delta^{13}$ C and  $\delta^{15}$ N values to quantify monthly shifts in C<sub>3</sub> versus C<sub>4</sub> resource use and trophic level (Wolf et al. 2009) at the UNM Center for Stable Isotopes. Body size is a surrogate for many life history attributes in animals (Sibly & Brown 2007). We will use our vehicle-based Quantitative Magnetic Resonance system to quickly (<2 min.) and non-invasively quantify rodent body condition, including total fat, lean mass, and total water content ,accurate to ±0.1g. We will use a portable ultrasound unit (Sonosite Titan) and field observations to quantify female rodent reproductive effort, timing, and duration (Gilman & Wolf 2007, Mathiasen et al. 2007).

Traits and diversity as predictors. Our methods allow for comparative analysis across species, communities, or ecosystems (see e.g., Hsu & Adler 2014b). We will test the hypothesis (Q2) that populations / communities / ecosystems dominated by species with resource-conserving traits will be less sensitive to climate change than those dominated by acquisitive traits. Model selection procedures (Burnham & Anderson 2002) will determine the most informative relationships between traits (Table 3) and climate sensitivity functions (linear and nonlinear coefficients) or antecedent effects (presence/absence via model fit, size via parameter estimates, Ogle et al. 2015). This allows for a wide range of hypothesis tests. For example, prior work supported the hypothesis that short-lived species are more sensitive to climate variance than long-lived species (Morris et al. 2008). In light of typical correlations between traits, and because we expect selection to operate strongly on the multivariate phenotype (Laughlin & Messier 2015, Muscarella & Uriarte 2016), we will also construct an index of multivariate trait conservatism  $(I_c)$  as follows. Each trait will be standardized to a mean of 0 and a standard deviation of 1, oriented so that negative values represent conservative values and acquisitive trait values are positive. For communities, the  $I_c$  will be community weighted using SEV abundance data for each species. We will calculate Ic for each plot in our Mean-Variance experiment, for existing quadrats in each biome, and for consumer datasets (Table 2). In addition to predicting sensitivities and antecedent effects, we will use Ic values to predict the amount of change in (1) biomass/abundance by species or community total, (2) community composition (e.g., Bray-Curtis distance between centroids of initial and final communities), and (3) biogeochemical or physical processes (e.g., [C]:[N], soil moisture). Change will be evaluated over the course of the (1) Mean-Variance experiment, (2) funding cycle interval in each biome (6 yr), and (3) period of record (e.g., Fig. 15). To test a hypothesis from (Q2) that higher trait variance buffers against climate variability, we will calculate standard metrics of trait variance (CV) and diversity (e.g., Shannon) for traits and species and use them to predict the amount of change in community composition, total biomass, or process rates, as described above.

Incorporating traits into models. (Luo, Wlicox) A SEV trait database will allow us to incorporate traits into our model framework, a cutting-edge method that can improve model prediction (Dietze et al. 2014). We will take two approaches to the integration of traits. First is forward modeling, in which we will modify TECO (see VI.) to allow dynamic adjustments of community-level traits as the species composition of the community changes. In this way, TECO keeps track of species abundances and their traits, especially when coupled with the WAVE model. For example, if black grama continues to increase in abundance in desert grasslands, TECO will dynamically adjust rooting depth to reflect the increasing influence of black grama relative to other community members. The second approach is inverse modeling under a Bayesian framework. We will use the observed trait mean and variance as *priors*; assimilation of multiple datasets can inversely update and estimate trait-related parameters to examine the influence of both inter- and intraspecific trait variation on ecosystem function.

*Trait and Evolutionary Monitoring Program.* (Cook, Mudge, Natvig, Smith, Taylor, Whitney) Our proposal to track evolutionary change in key traits and alleles leverages LTER strengths in historical ecology and represents an important enhancement of the LTER mission. We will implement a robust monitoring program for shifts in species traits and the evolutionary changes that underlie those shifts. Monitoring trait change is critical because altered trait distributions will shape how future populations and communities respond to ongoing climate change. The ongoing revolution in genetic sequencing technologies means that we are increasingly able to connect phenotypic changes in populations to genetic changes, even in non-model species.

Trait monitoring. We will test a hypothesis from (Q2) that long-term increases in climate mean and variance will shift trait distributions from acquisitive toward more conservative strategies. In the Mean-Variance experiment, we will monitor species composition changes and calculate the index of conservatism,  $I_c$  (see Traits and diversity as predictors, above) at yearly intervals. We will use repeated-measures general linear models to test for treatment effects on  $I_c$ . We will gain long-term perspective by simulating shifts in population and community trait distributions, based on predicted responses of species to changes in *SPEI* and soil moisture. We expect (Q2), a peak in trait variance at intermediate climate variance because of two opposing forces: fluctuation-dependent mechanisms that conserve variance vs. demographic or environmental stochasticity that eliminate variance. By monitoring species composition and traits in our Mean-Variance experiment and in SEV's five biomes, we will test this hypothesis via model selection procedures on linear/nonlinear models of trait variance regressed on climate variance.

*Evolutionary monitoring.* The LTER network represents untapped opportunity to monitor evolutionary response to changing climate. We will follow population *traits* and their underlying *genetic bases* via biome-specific collections (a) every 6 years, (b) in our Mean-Variance experiment, and (c) following climate extremes (Whitney, Mudge). Partnering with the Museum of Southwestern Biology (UNM) and National Center for Genome Resources (Santa Fe), we will archive and investigate the genetic histories of dominant species, using exact GPS coordinates for re-sampling. We will sample roots of 5 foundation plant species (to include their microbiome), 6 small mammal species (20% of total), 11 grasshoppers (20%), and soils containing 2 species of *Microcoleus*, the foundational cyanobacteria in biocrusts. For species with dormant storage (e.g. seeds, spores), we will adopt the seed banking methods of Project Baseline (Etterson et al. 2016). For microbes in biocrusts and in plant roots, we will gain a long-term record of shifts in microbial composition, particularly in response to climate. SEV's unique fossil record of woodrat middens, which has not yet been explored, will contextualize results in >20,000 years of vegetation history (Smith & Betancourt 2006, Smith et al. 1995, Smith et al. 1998). As genes for climate

adaptations are identified (Reusch & Wood 2007), we will use the newly archived materials plus extensive museum collections to assess molecular signatures of selection and shifts in allele frequency. During our first 6 years, efforts will be primarily archival. Future work will include projects to assess trait/genomic shifts in particular taxa. For example, periodic common gardens will compare ancestral vs. derived populations to evaluate trait evolution (Anderson 2016). Prior work indicates that significant evolutionary change in response to climate can occur even in 6 years (Franks et al. 2007).

*Proof-of-concept.* We have recently monitored evolutionary change in our extreme drought experiment (details provided below, **V. Disturbances**). An extreme drought in Chihuahuan Desert grassland (66% rainfall reduction for 3 yr) killed ~ 45% of the black grama grass. Using genotyping-by-sequencing (GBS), we compared the allelic



Fig. 20. Drought reduced genetic diversity in black grama grass (% of loci with 5X+ coverage that had >1 allele). *n*=10 plots / treatment.

diversity of live plants in drought vs. control plots, and of live vs. recently dead plants under drought. Drought reduced genetic diversity in both comparisons (by 7% & 11%, P = 0.005, 0.002; Fig. 20).

#### (IV.) Foundation Species Removals - Species Interactions and Biophysical Feedbacks-

In all SEV biomes, we maintain removals of foundation plants that allow us to test hypotheses for (**Q3**): *How will changes in climate variance and mean affect biome-specific biogeochemical processes and alter biophysical feedbacks*? These experiments provide a window on how biogeochemical and physical processes respond to the loss of foundation species. They also enable the collection of new demographic data in the presence/absence of competitors to inform our predictions of the trajectories of biome transitions (**Q1**) using our new WAVE model.

#### Grassland / Shrubland Removals. (D'Odorico, Miller, Peters, Sinsabaugh)

Removals were begun by D. Peters in 1995 for Great Plains grassland Core, Grassland Ecotone (Desert vs. Great Plains), Chihuahuan Desert grassland, Chihuahuan Desert shrubland, and Grass-Shrub Ecotone (Peters & Yao 2012). At core biome sites, the foundation species was manually removed from five plots (3mX4m), with five undisturbed controls (10 plots/site). At Ecotone sites, each co-dominant species was removed from a set of five plots (15 plots/site). Removal maintenance is performed annually

as needed. Yearly, during peak biomass (Aug-Oct), plant species richness and cover are visually recorded in each plot. LTER funds will support adding three new datasets: (1) Marking plants for yearly demographic censuses, (2) Installing soil moisture and temperature sensors, and (3) conducting periodic [C]:[N] analyses (Fig. 19) to monitor biogeochemical processes in these removals for the first time.

*Woodland / Savanna Removals.* (D'Odorico, Litvak, Pockman, Sinsabaugh, Taylor) A large-scale piñon girdling experiment initiated in 2009 (DOE DE-FG02-08ER46506, DE-SC0008088) removed >1600 piñon (all >7 cm dbh) in a 4 ha plot, a scale large enough to quantify biophysical feedbacks of piñon removal for the ecosystem using tower-based eddy covariance (Sinsabaugh, Litvak). External funds to support direct measures of C, water and energy fluxes, organismal physiology, and ecosystem structure in this site, and at a nearby piñon-juniper woodland used as a control will continue through 2020. Bark beetle/drought-triggered mortality of piñon in 2013 in our control site provides a comparison of ecosystem responses to natural vs. forced removal of this foundation species. In a newly funded experiment (NSF 1557176, Pockman, Litvak), we will remove either juniper or piñon in replicated 30mX30m plots in intact piñon-juniper woodland, then track responses of organismal physiology of the remaining species through sap flow, soil water availability, soil temperature, and understory species richness and cover. LTER will add (1) marked plants for demography and (2) [C]:[N] analyses of the stoichiometric landscape (Fig. 19).

# (V.) Disturbances: Abiotic and Biotic Modulators of Climate Change-

While our Mean-Variance experiment will alter climate variables fundamental to all dryland biomes, we also will re-envision ongoing, biome-specific experiments for which infrastructure is already in place. By layering long-term disturbances on top of a highly variable climate, we can evaluate (**Q5**) *How do disturbances alter the shape of climate sensitivities or the size of antecedent effects?* We focus on disturbances relevant to each specific biome: piñon mortality in woodlands, individual extreme drought events in grasslands, and in all biomes, fires, biocrust disturbance, and chronic N deposition. Because these datasets are ongoing, with infrastructure in place, LTER funding will mainly provide staff for maintenance and data collection. We predict that *abiotic and biotic disturbances will buffer or amplify ecological response to climate change by altering climate sensitivity functions and antecedent effects.* 

*All biomes: Atmospheric N deposition/fertilization.* (Collins, Natvig, Pockman, Porras-Alfaro, Sinsabaugh) Prior analysis of atmospheric bulk deposition data at SEV showed that N deposition was increasing and that components of N deposition are rather evenly split between NO<sub>3</sub> and NH<sub>4</sub> (Baez et al. 2007). We have two long-term fertilization experiments in SEV grasslands. The <u>NFert</u> began in 1995 as a cross-site test of effects on mycorrhizal fungi (Egerton-Warburton et al. 2007, Porras-Alfaro et al. 2007). In 2004-5, we began measuring plant species composition and belowground NPP (Ladwig et al. 2012). Thus far, inter-annual variation in above- and belowground production are not synchronized, N matters only in wet years, and N has few lasting effects on plant composition or diversity. SEV joined the Nutrient Network (<u>NutNet</u>) in 2007 (design protocol, Borer et al. 2014). These treatments include N, P, K additions in a fully crossed, randomized design with 5 replicates each. SEV data have been included in several NutNet publications (e.g., Adler et al. 2011, Firn et al. 2011, Hautier et al. 2014, Stevens et al. 2015). We are just approaching a long enough time series to compare climate sensitivity functions between controls and fertilizer additions. LTER funds will support long-term monitoring, so that we can make these comparisons.

*Factorial N additions in Mean-Variance experiment.* To understand interactions between climate manipulations and the chronic disturbance of N-deposition, 1m<sup>2</sup> subplots of resident vegetation in our Mean-Variance experiment will receive yearly N-additions, but stochastically. Ambient variance subplots will receive 3g/m<sup>2</sup> N per year. For increased variance plots, -50% reduction plots will receive 2g/m<sup>2</sup>N and +50% increase plots will get 5g/m<sup>2</sup> N, because the amount of rainfall affects the N deposition rate.

*All biomes: Fire*. (Collins, Finch, Ford, Friggens, Granillo, Litvak) While some prior work has examined antecedent climate effects on fire frequency (Abatzoglou & Kolden 2013, Urbieta et al. 2015), few studies ask whether fire affects nonlinearities in climate sensitivities, which could be essential to accurate prediction of future states. SEV has had 10 relatively large fires since 1993: 5 wildfires, 2 experimental burns, and 3 management burns. Long-term, post-fire monitoring includes >150 vegetation quadrats censused twice yearly as well as biogeochemical and soil erosion studies (Table 2). We have also tested

whether the seasonal timing of fire affects primary production; under natural drought, it did not (Ladwig et al. 2014). Those plots will be re-burned in 2017. A 2009 wildfire burned through a subset of long-term vegetation quadrats, a grassland flux tower, and some experiments (including NutNet). LTER funds will maintain long-term monitoring pre- and post-fire in both experimental and wildfire plots, allowing us to compare climate sensitivity functions and antecedent effects for burned vs. unburned ecosystems.

All biomes: Biocrust disturbance. (Garcia-Pichel, Porras-Alfaro, Rudgers) Biocrust disturbance plots occur in Chihuahuan Desert grassland and shrubland (*n*=10, Fig. 9). LTER funds will expand plots to piñon woodlands, juniper savanna, and Great Plains grassland. Disturbance occurs in May and September via two footsteps to 'stomp' each bare patch of the 6mX6m plots (similar to Kuske et al. 2012). Responses include 1mX1m vegetation quadrats, 2X yearly arthropod samples, 2X yearly archived (-80C) soil and root samples from foundation plants, and 6X yearly biocrust chlorophyll and scytonemin measures. At 3-yr intervals, we will assess leaf, rhizosphere, and biocrust [C]:[N].

**Extreme Drought in Grasslands Experiment.** (Collins, Mudge, Natvig, Pockman, Porras-Alfaro) This NSF-funded cross-site rainfall experiment imposes chronic drought during the growing season (Apr-Aug) with roof panels that cover 66% of each shelter (*n*=10, 6mX6m). A delayed summer monsoon is implemented by erecting full roof panels in Jul-Aug, capturing and storing rain during this time period, and reapplying it in 4-6 rain events during Sep-early Oct. Responses include air and soil temperature, soil moisture at two depths, soil CO<sub>2</sub> production and flux, belowground and aboveground production, and plant species composition. Ancillary work includes measurements of rhizosphere and biocrust microbial communities and plant evolutionary change (Fig. 20). The experiment is deployed in both Great Plains and Chihuahuan Desert grasslands at SEV, as well as in shortgrass steppe in Colorado and Wyoming, mixed grass prairie in central Kansas and tallgrass prairie in NE Kansas. LTER funds will support continued SEV monitoring to detect effects of drought on climate sensitivities and antecedent effects.

Woodlands: Mass mortality of piñon pine. Details provided in (IV. Foundation Species Removals)

### (VI.) Modeling Framework

#### Integration.

We will integrate our empirical work with dynamic models that span producers and consumers at population, community, and ecosystem levels. The motivation for data-model interface is two-fold. First, the models will function as tools for data analysis and integration, allowing us to project responses to manipulations of climate mean and variance at scales that cannot be directly observed. For example, the models enable tests of whether increased climate variance will accelerate or decelerate biome transitions (**Q1**), even though these transitions may play out over decades or centuries. Second, the models will function as tools to explore regions of parameter space that are not represented in our experiments, facilitating general inferences that transcend the particular conditions of our empirical work. In this way, we will use models to explore the impacts of climate variance that is more or less extreme than will be imposed in the Mean-Variance experiment.

Our three models predict: (1) the spatial trajectories of biome transitions (WAVE, **Q1**), (2) the ecosystem processes that result from plant community trait distributions and biome transitions (TECO, **Q2-3**,



Fig. 21. SEV models with color-coded datasets used in each. WAVE predicts state transitions that determine TECO inputs. TECO predicts ecosystem changes that feedback to competition & demography in WAVE. TECO predicts altered resource availability to drive consumer dynamics in SDP.

**5**), and (3) the influence of climate and plant community composition on consumer fitness and population dynamics (SDP, **Q4**). Each model can stand alone to address the effects of climate variability on biome transitions, ecosystem processes, and consumer dynamics, respectively. Importantly, we will use these models to inform each other (Fig. 21). WAVE predicts the trajectories of foundation plant species, which, in turn, control community trait distributions. By incorporating predicted state transitions and associated trait distributions into TECO, we will link plant community changes to ecosystem process rates. We will use outputs from TECO to feed back to WAVE to modify demographic transitions and competitive

dynamics of foundation plants based on mechanisms of biophysical feedbacks (e.g., soil moisture profile). Since ecosystem processes and biome transitions will determine food abundance and quality, results from the WAVE/TECO interface will drive consumer dynamics in SDP. Altogether, we will use these models to provide an integrated understanding of how and why drylands respond to changes in climate mean and variance across levels of organization. A unique feature of our modeling component is that we will use the Bayesian framework to assimilate data from the experiments and observations. This allows us to constrain the models and fully quantify uncertainty in a workflow that forecasts the long-term trajectories of SEV populations, communities, and ecosystems. Below, we describe each model in detail.

#### Ecotone Model (WAVE).

We will use WAVE to understand the dynamics of ecotones and their responsiveness to environmental variability across SEV's five biome types (Table 1). WAVE will allow us to address (**Q1**) by predicting the direction and pace of biome transitions under current and future regimes of climate variability, and by testing whether variability will generally accelerate or delay shifts from current to future foundation species. To forecast long-term spatio-



Fig. 22. Dispersal and competition elements of WAVE.

temporal dynamics in the mechanistic WAVE framework, we will integrate observational and experimental field data with regularly updated, regionally downscaled climate projections (Coupled Model Intercomparison Project, Fuentes, Gutzler).

Justification for the approach. Our goal is to understand the dynamics of dryland ecosystems and their ecotones, where foundation species "collide". Thus, we require a model that incorporates the two key features of this collision: dispersal and competition (Fig. 22). Patterns of dispersal govern the rate at which propagules (seeds) of one foundation species recruit into adjacent habitat dominated by another foundation species. Intra- and inter-specific competition then determine the fates of recruits that occur at low density in their own and their competitor's habitat. The long-term trajectory of an ecotone between two foundation species should therefore reflect a tension between the forces of dispersal moving seeds across habitats and inter-specific competition potentially suppressing the performance of long-distance dispersers that cross habitat boundaries (Fig. 22). Our novel WAVE model captures these forces in a simple and general framework that is well suited to applications across diverse ecotones at the SEV and in drylands globally. While approaches to ecotones historically focus at patch or landscape scales (e.g., Stewart et al. 2014), our WAVE model will yield novel insight by revealing the demographic and dispersal mechanisms by which individual-level responses to climate scale up to affect landscape composition.

Current theory suggests multiple, non-exclusive hypotheses for (**Q1**). First, a decrease in mean *SPEI* may promote expansion of some biomes at the expense of others (e.g., Chihuahuan Desert biomes encroaching on Great Plains grassland, see Domain). We predict in (**Q2**) that an increase in the variability of *SPEI* will favor the expansion of foundation species whose traits result in convex climate sensitivity functions and retraction of species with concave functions. Interactions between variability in *SPEI* and changes in mean *SPEI* may determine some ecotone trajectories. For example, our estimated climate sensitivity functions (Fig. 7) predict that variability will favor the expansion of Chihuahuan Desert grassland (black grama) into Great Plains grassland (blue grama) at low mean *SPEI*, but reverse this trajectory at high mean *SPEI*, with Great Plains grassland displacing desert grassland. Finally, theory predicts that greater environmental variability can increase the potential for competitive coexistence via fluctuation-dependent mechanisms, such as the storage effect and relative nonlinearity of competition (Chesson 2000). This theory suggests that higher variability may increase species mixing, essentially promoting expansion of both waves in the collision (Fig. 22). The WAVE model will provide a quantitative framework for evaluating these competing hypotheses for effects of climate change on ecotone dynamics.

WAVE Methods details. Our WAVE model is built upon well-developed ecological theory for the spread of single populations (Andow et al. 1990, Kot et al. 1996, Neubert & Caswell 2000, Okubo & Levin 2002, Skellam 1951). This theory predicts the velocity of a single expanding wave based on the probability distribution of dispersal distances (or "kernels") and the regeneration potential of long-distance dispersers, under the assumption that the population is spreading into empty habitat. To extend theory to ecotones, we consider two population waves of foundation species "colliding" in a saturated landscape. SEV biome transitions occur over spatial gradients where alternative foundation species trade off in



Fig. 23. Example of collision zone along a permanent transect spanning the shrubland-grassland ecotone. Creosote-dominated (left photo), mixed (middle photo), and black-grama-dominated (right photo) habitats.

abundance, consistent with a wave collision framework (Fig. 23). The long-term ecotone trajectory should thus depend upon whether, in which direction, and at what rate each foundation species is moving.

Our approach is based on integrodifference equations (IDE, Kot et al. 1996) for population growth in discrete time and continuous, homogenous, and one-dimensional space. Alternatively, previous studies have used individual-based cellular automata models to analyze ecotone dynamics (reviewed in Jiang et al. 2015). Individual-based models can be a powerful way to identify spatial patterns that emerge from specific biological processes (Sternberg et al. 2007, Teh et al. 2008). But, because they are defined by specific

mechanisms, these models can be difficult to generalize across systems. By relying on general principles of demography, competition, and probabilistic movement, WAVE is well suited for applications across the diversity of SEV ecotones (Table 1). Further, the mathematical framework of the WAVE model can be implemented as an individual-based simulation (Adler et al. 2010), providing flexibility to accommodate greater realism (soil heterogeneity, prevailing directions of wind dispersal, etc.) where appropriate. A traditional, single-species IDE assumes invasion into an empty landscape (Kot et al. 1996). Our WAVE model extends classic IDE theory to account for competition at the interface of two invasion waves.

Details of the full WAVE model are provided in Box 1, which represents size-structured plant populations with localized competitive interactions. The demography-dispersal kernel dictates probabilistic rules for demographic transitions within the size distribution (growth, survival, reproduction) and movement in space (seed dispersal). Functions for demographic transitions take as input variables local con- and hetero-specific densities to account for the competitive neighborhood, climate (SPEI) values, and random spatial and temporal heterogeneity. Competition is a spatially explicit process, where competitive neighborhoods are defined by a spatial contact function, estimated from field data (Box 1). For each pair of current and future foundation species (Table 1), analysis of the model (based on numerical simulation) will provide predictions about the direction and pace of change in the spatial position of the ecotone (m/yr). We will use a hierarchical Bayesian statistical framework to propagate estimation error and process variability into our projections for ecotone dynamics (Elderd & Miller 2016). vielding posterior probability distributions for velocities of colliding foundation species. If an ecotone is stationary in the long term, we expect both distributions to include zero. This approach will be repeated for the four treatments of the Mean-Variance experiment (Fig. 17) to test the prediction under (Q1) that shifts in climate mean and/or variance will modify ecotone dynamics. The WAVE model incorporates spatio-temporal variability in the abiotic environment (Box 1), including our key climate driver SPEI, and therefore can accommodate the realistically noisy wave shapes and sporadic advances of habitat boundaries that are thought to characterize dryland ecotones (Moreno-de las Heras et al. 2016).

WAVE Parameterization and integration of datasets. Dispersal: We will use species-level trait data (seed release height and terminal velocity) and wind properties measured at SEV met stations and towers to indirectly estimate seed dispersal kernels for each foundation species, following established methods based on fluid dynamics (Katul et al. 2005). Demography and competition: For each biome included in the Mean-Variance experiment, we will introduce seeds and seedlings of hypothesized future foundation species into experimental plots dominated by current foundation species (Table 1). This approach simulates the invasion dynamics of habitat collision. We will track demographic vital rates (survival, growth, reproduction) of naturally occurring and experimentally introduced individuals of each foundation species in the Mean-Variance plots. By leveraging natural and experimental variation in species densities across all plots, biomes, and in our foundation species removals, we will be equipped to quantify the intra-and inter-specific competitive interactions that are core to the WAVE model (Box 1).

WAVE Customization and validation. The basic WAVE model assumes that ecotones arise solely from competitive interactions at a habitat interface, and that the environmental context underlying the ecotone is homogenous. Alternatively, some ecotones may be driven partially or predominantly by

environmental gradients. We will modify the WAVE model to relax the assumption of environmental homogeneity, where appropriate. We will validate the predictions of the WAVE model in two ways. First, our long-term data and remote sensing datasets allow us to estimate historical ecotone transition or stasis. We will compare these independent observations to WAVE model predictions based on the historical climate mean and variance. Second, the competition-dispersal kernel of the WAVE model (Box 1) is expected to generate characteristic shapes of colliding "waves" of foundational species. We will compare predicted and observed wave shapes as an additional validation criterion.

Box 1. WAVE model to study ecotone dynamics under non-stationary environmental variability. The model describes space and size dynamics of two foundation species at their habitat interface (i and j; only expressions for species *i* are shown). The state variable  $n^i$  gives the density of individuals at a particular size, location, and time. The kernel  $K^i$  describes all possible transitions from size u, location x, time t to size v, location v, time t+1 based on the combination of local competition and dispersal. The kernel is integrated over size and space.

$$n^{i}(v, y)_{t+1} = \int \int K^{i}\left(u, v, x, y, \widetilde{n(x)_{t}^{u}}, \widetilde{n(x)_{t}^{u}}, \boldsymbol{S}, \boldsymbol{\theta}\right) n^{i}(u, x)_{t} \, du \, dx$$

The space-size projection kernel  $K^i$  combines functions for seed dispersal, fertility, survival, and growth. Local demography functions include local con- and hetero-specific densities weighted by size  $(\widetilde{n(x)})$ , a vector of SPEI or soil moisture values (S) representing inter-annual variation, and a list of random deviates ( $\theta$ ) reflecting random temporal and spatial heterogeneity ("process error") unrelated to moisture.

Dispersal kernel for  
a plant of size *u*. Production of *v*-siz  
*u*-sized maternal *p*  
$$n(x)^{u}$$
  $n(x)^{u}$  **S A**  $= D^{i}(|x - y||_{u}) + E^{i}(|x - y||_{u}) + E^{i}(|x - y||_{u})$ 

Production of v-sized recruits from lants.

$$K^{i}\left(u, v, x, y, \widetilde{n(x)_{t}^{u}}, \widetilde{n(x)_{t}^{u}}, \boldsymbol{S}, \boldsymbol{\theta}\right) = D^{i}(|x - y|, u) \cdot F^{i}\left(v, u, \widetilde{n(x)_{t}^{u}}, \widetilde{n(x)_{t}^{u}}, \boldsymbol{S}, \boldsymbol{\theta}\right)$$

$$+\delta_0(|x-y|)\cdot S^i\left(u,\widetilde{n(x)_t^{i_l}},\widetilde{n(x)_t^{i_l}},\boldsymbol{S},\boldsymbol{\theta}\right)\cdot G^i\left(v,u,\widetilde{n(x)_t^{i_l}},\widetilde{n(x)_t^{i_l}},\boldsymbol{S},\boldsymbol{\theta}\right)$$

The delta function prevents movement of stationary life stages.

Survival probability for a plant of size *u*. Probability of growth from size *u* to size *v*.

Size-weighted density of species *i* is integrated over a neighborhood, where  $\alpha_{ii}$  defines how the effect of j on i declines with distance (x-z). C is an integration constant.

 $\widetilde{n(x)_t^{ij}} = \int \int (n^j(u,x)_t \cdot u) \ e^{-\alpha_{ij}(|x-z|)^2} / C \ du \ dz$ 

Terrestrial ECOsystem Model (TECO). We will develop a new dryland version of the ecosystem model TECO (Weng & Luo 2008) that will assimilate SEV data and constrain predictions of ecosystem responses to climate trends and variance. We will use the TECO model to predict ecosystem dynamics into the future and explore parameter space beyond what we can manipulate to address (Q3), which examines responses of biogeochemical processes and biophysical feedbacks and (Q5), which tackles ecosystem responses to climate variability following disturbances. Our new front-end to TECO will link traits to ecosystem processes to better understand (Q2), why are some biomes more sensitive to climate mean and variance than others? By varying trait distributions in TECO simulations, we can evaluate how trait change alters ecosystem sensitivity to climate over long time periods. We have the distinct advantage of 10+ years of ongoing tower flux data from each biome, which aid in both parameterization and validation of TECO.

Justification for the approach. TECO is a typical terrestrial ecosystem model that simulates biophysical and biogeochemical processes in ecosystems. TECO has been used successfully to quantify the main and interactive effects of climate warming, altered precipitation, and elevated [CO<sub>2</sub>] on net primary production (NPP), heterotrophic respiration (Rh), net ecosystem production (NEP), transpiration, and runoff in a variety of biomes (e.g., Luo et al. 2008, Xu et al. 2015a). In addition, we have used TECO in model inter-comparison projects with a dozen other ecosystem models at 22 AmeriFlux sites and several CO<sub>2</sub> experiments (De Kauwe et al. 2013, Gao et al. 2011, Schwalm et al. 2010, White & Luo 2002). We have largely focused so far on predicting responses to changing mean climate. Planned work adds novelty by considering the mean × variance interaction, which is particularly relevant for drylands.

A distinct advantage of TECO is that it can be used effectively in a data assimilation (DA) framework (described below). Luo (co-PI) and his group have used TECO with data assimilation in the Duke Forest CO<sub>2</sub> Experiment, Oklahoma and Alaska warming experiments (Luo et al. 2011, Luo & Weng 2011, Shi et al. 2015a, 2015b), FluxNET syntheses (e.g., White et al. 2006, Wu et al. 2009), continental and global inventory data of biomass and soil C content (e.g.,Hararuk et al. 2015, Zhou & Luo 2008, 2015), soil respiration from field measurement (Luo et al. 2001), and soil incubation data (e.g., Liang et al. 2015, Xu et al. 2016). In addition, Luo recently coupled TECO with the Ecological Platform for Assimilating Data into models (EcoPAD) to enable real- or near-time forecasting at the DOE ORNL Spruce and Peatland Responses Under Climatic and Environmental Change (SPRUCE) site in northern Minnesota. Various datasets, including data streams for meteorological data, water table, phenology, and respiration, plus discrete measurements of C flux, above- and belowground biomass, and soil carbon content, have been assimilated through EcoPAD to constrain the TECO model (Jiang et al. in prep.) to project future ecosystem responses to warming and elevated [CO<sub>2</sub>]. Techniques we developed for SPRUCE are directly transferable to the new SEV drylands model.

Description of the TECO Model. TECO has five major components: (1) canopy photosynthesis, (2) soil water dynamics, (3) plant growth, (4) litter and soil C decomposition and transformation, and (5) N dynamics as described in detail by Weng and Luo (2008). Canopy photosynthesis is referred from a twoleaf (sunlit and shaded) model developed by Wang and Leuning (1998). This submodel simulates canopy conductance, photosynthesis, and partitioning of available energy. The model combines the Farguhar model (Farguhar et al. 1980) and a stomatal conductance model developed by Harley et al. (1992). In the soil water dynamic submodel, soil is divided into 10 layers. Soil water content (SWC) of these layers is determined by the mass balance between water influx and efflux. The plant growth submodel simulates carbon allocation and phenology. Allocation of the carbon among different plant components depends on their growth rates. Phenology is related to leaf onset, which is triggered by growing degree days, and leaf senescence, which is determined by temperature and soil moisture. The transfer submodel estimates carbon transferring from plants to litter and three soil layers. The nitrogen submodel is fully coupled with carbon processes with one additional mineral N pool. N is absorbed by plants from mineral soil and partitioned among leaf, woody tissues, and fine roots. N in plant detritus is transferred among different ecosystem pools (i.e. litter, fast, slow and passive SOM) (Shi et al. 2016). The model is driven by climate data (incl. air and soil temperature, vapor-pressure deficit, relative humidity, incident photosynthetically active radiation, and precipitation) at hourly steps.

*Data Assimilation (DA).* Luo lab was among the first to develop and apply DA techniques (Box 2) to ecological research with TECO and other models (Luo & Reynolds 1999, Luo et al. 2001, Luo et al. 2009, Xu et al. 2006). DA uses data to inform initial conditions and model parameters, thereby constraining a model during simulation to yield results that approximate reality as closely as possible (Luo et al. 2011). Luo lab has developed and applied a wide variety of DA techniques that will be tailored for use in our proposed dryland TECO model (Gao et al. 2011, Luo et al. 2003, White & Luo 2002, Wu et al. 2009, Xu et al. 2006, Zhou et al. 2008). To minimize deviations between model predictions and observations, we search for optimal target variables (eq. 2, Box 2) using an optimization technique. For example, the Markov chain Monte Carlo (MCMC) technique uses a Markov chain with Gibbs sampling and/or Metropolis-Hastings (M-H) algorithm to sample target variables. Once the chain has been simulated for a sufficiently long period so that the distributions of target variables follow stationary states, samples from the simulations are collected to approximate the distributions of the target variables within a Bayesian framework (eq. 2, Box 2, Xu et al. 2006). The generated posterior distributions of target variables can be used to determine most probable values, mean values, quantiles, and other metrics of uncertainty.

**Box 2.** Data assimilation (DA) combines data with a model by updating model parameters and/or selecting alternative model structures (i.e., target variables) using optimization techniques to generate posterior simulations. Optimization procedures involve a cost function that quantifies the deviation (*e*) between modeled and observed values with multiple data sets as:

$$e_i(t) = Z_i(t) - \varphi_i X(c, t)$$

(1)

where  $Z_i(t)$  is an observation of the *i*<sup>th</sup> data set and  $\varphi_i X(c, t)$  is the corresponding modeled value at time *t*. The modeled value is usually related to state variables of the model, X(c, t), using a mapping function  $\varphi_i$  that relates the modeled variable to its observed counterpart. *c* represents target variables, which could be parameters or model structures (e.g., a set of difference functions) to be optimized. The deviation is usually termed an error and results from inaccurate observation, an imperfect model, or both. By

adjusting the target variables (c) the modeled value  $\varphi_i X(c, t)$  and consequent deviation (i.e., error), e(t), vary. Thus, we can define a cost function, J(c), with multiple data sets as:

 $J(c) = [Z_i(t) - \varphi_i X(c, t)]^T cov(e(t)[Z_i(t) - \varphi_i X(c, t)]$ (2) where cov(e(t) is a covariance matrix for vector e(t). The non-diagonal elements in the matrix cov(e(t) represent correlations between different error components, while the diagonal elements specify variances of the components of e(t), which can be estimated from observations (Luo et al. 2003). The likelihood function p(Z|c) is then defined as:

 $p(Z|c) \propto \exp(-J(c))$ 

(3)

Then, with Bayes' theorem, the posterior probability density function of parameters c is given by  $p(c|Z) \propto p(Z|c)p(c)$  (4)

where p(c) is the prior probability density function of the parameters.

Ecological forecasting. In this rapidly changing world, improving the capacity to forecast future dynamics of ecological systems and their services is essential for better stewardship. Forecasting relies on models that describe our understanding of the major processes that underlie system dynamics and data about these processes and the present state of ecosystems (Niu et al. 2014). Forecasting becomes more effective when models are well informed via DA. Luo lab has collaborated with computer scientists and developed a DA System (Ecological Platform for Assimilating Data, EcoPAD) for such forecasting. EcoPAD consists of: (1) multiple sources of data, (2) ensemble of ecosystem models, (3) DA algorithms, and (4) workflow to automate data fetch, model execution, and other functionality. The workflow of EcoPAD starts with ecological data to be captured from data sources via either manual operation or scheduled automation from sensors. The data are described and metadata captured via the EcoPAD metadata catalog. Attention is paid to how a particular dataset varies over space (x, y) and time (t). This spatiotemporal variability is described and placed in a metadata catalog with guery capability (via REpresentational State Transfer (REST) application program interface (API)). Models written in varied programming languages are described by a series of wrapper tasks (Python code). Then, a model can be executed from a RESTful API by specifying datasets and model parameters. Researchers have a common access point for model results, model-specific data requirements, and model run metadata. All model input / output will be available for download.

*TECO Preliminary results.* As proof of concept, we used TECO to project ecosystem functioning under scenarios of altered mean and variability of climate. We compiled 13 years (2000-2012) of hourly weather data with net primary production (NPP) data from a SEV desert grassland to calibrate the TECO model. Across the 13 years, observed ANPP was 97.5 ± 21.1 g/m<sup>2</sup> (mean ± s. e.) and TECO-simulated ANPP was 95.0 ± 5.0 g/m<sup>2</sup>. We cycled weather data for 100 years to spin up the model, at which point soil C and biomass pools were stable. We then modified 2000-2012 weather data to reflect two climate scenarios: (1) To reduce mean soil moisture ( $\theta$ ) (increase the mean drought index, +Mean), we increased



Fig. 24. TECO forecasts for GPP under altered climate mean and variance; bars are means  $\pm$  s.e. of 5 unique replicates.

air temperature by ~4°C throughout each year, and (2) to increase  $\theta$  variability (**+Variance**), we decreased all precipitation events by 50% in drier than average years, and increased precipitation events by 30% in wetter than average years. The result was a near doubling of the coefficient of variation of annual precipitation (*CV:* Ambient= 0.26, +Variance= 0.51), without changing the mean (Ambient= 241.1 ± 6.8 mm, +Variance= 253.4 ± 13.6 mm). The  $\theta$  variability scenario was designed to examine antecedent effects of environmental stochasticity that usually cannot be captured in global change studies. (3) We combined altered mean and variance of  $\theta$  (**+Mean+Variance**) to test for mean × variance interactions. We generated five independent replicates of 100 random draws from each climate scenario.

TECO runs of these 100-year weather compilations showed greater gross primary production (GPP, Fig. 24), aboveground net primary production (NPP) and belowground NPP responses to altered mean climate than to altered variance. However, ecosystem respiration (ER) was also higher with increased mean climate, producing a moderate increase in net ecosystem exchange (i.e., a stronger C source). These increases in NPP and ER with warmer air temperature are counterintuitive, because higher evaporation rates should reduce soil moisture and thus reduce ecosystem functioning. However, preliminary model projections suggested that increased temperatures may extend the time period when plant growth is not limited by temperature, so when rains come in early spring/late fall, a longer growing season results in higher NPP. *These findings highlight the need to empirically test multiple aspects of climate impacts, because they deviate from predictions based on the climate sensitivity functions derived from SEV long-term data (Fig. 7).* Proposed work will explore causes of divergence between model results, long-term observations, and results from our Mean-Variance experiment, using SEV flux tower data and other sources to constrain predictions (Anderson-Teixeira et al. 2011). We will use model simulations such as these to formulate and refine hypotheses, test them with empirical data, and then update these new models for dryland ecosystems.

TECO Modeling, data assimilation, and ecological forecasting at SEV. Building upon preliminary analysis (Fig. 24), we will do modeling in close collaboration with the Mean-Variance experiment and observations from flux towers, remote sensing, and biogeochemical measurements. The dryland version of TECO will explicitly include microbial processes and enable simulations of biogeochemical processes in biocrusts. The new microbial submodel will incorporate extracellular enzyme activities (C, N, and Pacquiring) and carbon use efficiency (CUE) (Moorhead et al. 2012, Moorhead et al. 2013, Sinsabaugh et al. 2013, Zechmeister-Boltenstern et al. 2015). We will estimate realized microbial CUE as a tradeoff between net energy acquisition from hydrolyzing polysaccharides (cellulose) and net energy cost of oxidizing polyphenols (lignin) as in the Guild Decomposition Model (Moorhead et al. 2014). This microbial version of TECO will permit us to explore plant-microbe interactions at SEV. We will further develop TECO by incorporating the proposed SEV plant traits database to predict ecosystem dynamics during biome transitions. We will also use DA techniques to assimilate data from the experiments and observations to train the TECO model before we use it to explore how ecosystem productivity and biogeochemical processes respond to (1) changes in climate means and variability, (2) disturbances, and (3) resulting biome transitions. Moreover, we will adopt EcoPAD to develop real- or near-time ecological forecasting, first at our flux tower sites, and later for our Mean-Variance experiment. This ecological forecasting system will feed back to inform both what datasets are needed to improve predictive ability and what modeling improvements are required.

#### Consumer Stochastic Dynamic Program (SDP).

We will use a novel Stochastic Dynamic Programming model (SDP) to address (**Q4**) *How do climatedriven changes in dryland resources affect consumer population dynamics*? SDP couples core LTER datasets of plant and consumer abundance with ongoing measurements of consumer traits, diet composition, body condition, and fecundity to predict how future climates will impact consumers in dryland ecosystems and their ecotones. Because water severely limits primary production in dryland ecosystems (Noy-Meir 1973), these systems are strongly regulated by bottom-up processes, which in turn regulate consumer population dynamics (Brown & Ernest 2002, Yates et al. 2002)

*Justification for the approach.* We adopt a SDP approach (Marescot et al. 2013) for several reasons. (1) For consumers living on the edge, it is critical to model the <u>energetic state</u> of the animal. (2) SDPs hierarchically link multiple variables that influence this state, including <u>stochastic</u> environmental conditions, resource availability, and consumer traits. (3) SDPs incorporate *a priori* <u>mechanisms</u> affecting foraging behavior, body condition, and fecundity to define fitness functions, shedding light on underlying drivers of the well-documented correlations between dryland consumer dynamics and rainfall (Brown & Ernest 2002, Thibault et al. 2010). (4) Because fitness is the common currency, we can use fitness-maximizing behaviors used for resource procurement to <u>estimate population growth rates</u>, allowing us to forecast how climate variance and mean affect consumer dynamics from the causal mechanisms.

*Consumer traits, diversity and dynamics.* Despite the stochastic nature of resource availability, drylands often support diverse consumer communities (Fox 2011) with a wide range of traits and lifehistory strategies for resource procurement (e.g., caching behavior, foraging guild) (Ernest 2005, Supp et al. 2015). For example, Heteromyid rodents (e.g., *Dipodomys* spp.) are food-caching granivores that range in body size from ~5–125g and have conservative traits such as long gestation times and small litter sizes. Heteromyids typically out-compete other species for high-quality seeds and store food in caches that can persist across seasons and even years (Schroder 1979, Vander Wall 1990). In contrast, Cricetid rodents such as deer mice (*Peromyscus* spp.) and grasshopper mice (*Onychomys* spp.) do not hoard food at the SEV and must forage continuously to survive, but they can occupy multiple trophic levels. With acquisitive traits, like shorter gestation times and larger litter sizes, Cricetids typically have higher reproductive potential than sympatric Heteromyids, but are more prone to population crashes (Hoffmeister 1986). In particular, caching behavior is a vital trait in the context of environmental stochasticity because it can allow consumers to buffer against periods of resource scarcity, which may reduce species extinction risk. *Our hypotheses for (Q4) are that consumers with resource-conserving traits will be less sensitive to climate change than those with acquisitive traits, and consumer species with higher trait variance and diversity will be less sensitive than those with low trait variance.* 

Species-specific SDP models will determine which foraging decisions maximize fitness under different climatic, competitive, and predation scenarios. Our SDP will use SEV long-term and short-term data to yield a new theoretical framework for understanding and forecasting dryland consumer dynamics. Traditional mark-recapture and count data will continue to estimate survival, density, and population size of small mammals and grasshoppers (Table 2) to <u>validate</u> SDPs (Marescot et al. 2013), and aid in linking individual fitness to long-term population dynamics. <u>New measurements</u> will include (1) diet composition via stable isotope analysis, (2) body condition via field-based quantitative magnetic resonance, and (3) estimates of fecundity via visual inspection and ultrasound to inform models (methods in III. Traits). Other proxies such as scat DNA metabarcoding provide greater diet resolution (e.g., Kartzinel et al. 2015); however, these genetic techniques do not yield temporally integrated information on resource assimilation without exhaustive and expensive sampling designs. Further, isotope analysis of consumers and their resources will yield robust seasonal estimates of the relative proportions of C<sub>3</sub> (shrubs and forbs) vs. C<sub>4</sub> (grass) vs. insects consumed by each species, informing our SDP and making it easy to integrate with outputs from our ecosystem model, TECO.

How the consumer SDP works. In our framework, an individual must maintain homeostasis while establishing a buffer of endogenous (fat and lean mass) and/or exogenous (caches) reserves to survive a stochastically varying environment. Foraging decisions maximize the individual's future fitness integrated over the course of its lifetime, thus predicting fitness-maximizing behaviors that represent the evolutionary endpoint of natural selection. The goals involve determining: (1) which resource type (C<sub>3</sub> vegetation, C<sub>3</sub> seeds, C<sub>4</sub> vegetation, C<sub>4</sub> seeds, or insects) maximizes an individual's fitness with respect to its age and current endogenous and exogenous energetic state, (2) whether a given resource should be consumed or cached, and (3) the fitness changes due to different behavioral strategies which inform the population growth rate. Preliminary work has focused on rodents but will be modified for SEV grasshoppers (e.g., Boggs 2009). We model the foraging decisions of an organism as a function of 3 principle state variables: (1) time *t* at which a foraging decision is made, (2) the net endogenous energetic reserves at time *t*, X(t) = x, and (3) the net exogenous energetic (cache) reserves at time *t*,  $\Theta(t) = \theta$ , where a unit change in *x* or  $\theta$  is 10 kJ. Here, upper case notation refers to stochastic variables, and lower case refers to particular values. For mammals, units for exogenous and endogenous stores are of like currency because the cache accounts for only the consumable energetic yields of stored resources.

INPUTS FITNESS FUNCTION (W)			- OUTPUTS	
	Terminal Fitness Funct	ion: $W(x, \theta, t = T) = \Psi(x, \theta);$		
1) Resource Encounter Rates Seasonal ANPP (g/m²) Home Range (ha)	$W(x, \theta, t < T) =$ $(1 - p_{\mu})\max\left[p_{K}(k = 0)\right]$	consume from cache $y_{j} \widetilde{W(X(t) - aM^{b} + Y_{\theta}, \Theta(t) - Y_{\theta} - \delta, t + 1)}$	1) Resource Selection C <sub>3</sub> Leaves/Seeds C <sub>4</sub> Leaves/Seeds Insects	
2) Resource Energy Content Energy Content (kJ/g) Digestibility (% dry mass) Protein Content [N] Seed Size (g)	$+\sum_{k=1}^{k_{max}}p_{K}(k)_{j}\mathrm{n}$	$\max \{ \overbrace{W(X(t) - aM^b, \Theta(t) + Y_k - \delta, t+1)}^{\text{cache resource}}; $	2) Energetic Strategy Consume-Endogenous (kJ) Cache-Exogenous (kJ)	
3) Allometric Constraints	t = Time (day)	consume resource	3) Adult Survival	
Metabolic Costs ~ aM <sup>b</sup> (kJ) Stomach and Pouch Size Starvation Threshold	$\theta$ = Cache Reserves (10kJ)	$W(X(t) - aM^{\circ} + Y_k, \Theta(t) - \delta, t + 1) $	4) Reproductive Output	
	x = Energetic Reserves (10kJ) Y <sub>0</sub> = Cache Yield (kJ) Y = Resource Yield (kJ)	m = Mass(g) a/b = Allometric Constants $p_{ii} = \text{Probability of Mortality}$	5) Population Status	
	$\delta = \text{Decay Constant}$	$p_{K}^{F}(k)_{j}$ = Probability of Encounter k grams of Resource j		

Fig. 25. Schematic of the stochastic dynamic program (SDP) used to calculate the decision array  $D(x, \theta, t)$  (see Fig. 26); it will form the basis for a population dynamics model based on fitness-maximizing foraging decisions.

*Proof-of-concept.* We built a preliminary SDP for the kangaroo rat, *Dipodomys merriami*. We set the maximum endogenous energetic storage ( $x_{max}$ ) to equal the energetic yield contained in both lean and fat body mass (316 kJ for a 40g *D. merriami*), while the minimum determines the starvation threshold  $x_c = \eta x_{max}$ , where η is the proportion of non-consumable body tissue, scaling as  $M^{1/4}$ , below which starvation occurs. The cache is not limited by body size, such that  $\theta_{max} > x_{max}$ , and minimum cache size is 0. At each time step, there is energetic loss via metabolic costs ( $aM^{3/4}$ ), where *M* is body mass (g) and *a* is the metabolic intercept. Similarly, the cache is not static; it can decline due to decay and/or theft ( $\delta$ ). We then assume that 3 potential behaviors determine the forager's interaction with a given resource, conditioned on whether a particular resource is found in the time interval: (1) if the resource is not found, the forager consumes from its cache, where the yield is bounded by daily digestive capacity  $x_s$  (Y<sub>θ</sub> = min[ $\Theta(t)$ ,  $x_s$ ]; red eq. in Fig. 25); (2) if the resource is found, it can either store the yield ( $Y_k$  = min[energetic gain of food *j*,  $x_p$ ]) in its cache, bounded by  $x_s$  ( $Y_k$  = min[energetic gain of food *j*,  $x_s$ ]; green eq. in Fig. 25). Whether a resource is consumed by  $x_s$  ( $Y_k$  = min[energetic gain of food *j*,  $x_s$ ]; green eq. in Fig. 25).

Stochastic environmental conditions such as precipitation and associated plant production impact predicted foraging behaviors by modifying the distribution and abundance of resources, thereby altering the likelihood of finding food type *j*. We let the random variable *K*=*k* represent the amount of resources (in grams) found within a particular interval. With probability  $p_K(k)_j$  an individual finds *k* grams of food type *j*, where  $p_K$  is distributed as a Negative Binomial with mean  $m_j$  and dispersion  $v_j$ . We used SEV plant biomass data to parameterize  $m_j$  and  $v_j$  for both winter/spring and summer monsoon seasons. We assume that the probability of mortality from predation  $p_\mu(m,v)$  is contingent on habitat structure informed by C<sub>3</sub> (shrubs and forbs) versus C<sub>4</sub> (grass) resource distributions. In the winter/spring, C<sub>3</sub> standing biomass dominates, while during the monsoon C<sub>4</sub> biomass dominates. In both cases, we assume that C<sub>3</sub> and C<sub>4</sub> vegetation are more evenly distributed (high dispersion;  $v_j = 10$ ) than C<sub>3</sub> and C<sub>4</sub> seeds ( $v_j = 5$ ), while insects are highly patchy (low dispersion;  $v_j = 1$ ). Finally, the energetic gain of a particular food must be modified by its digestibility ( $\epsilon$ ), which varies across food groups: C<sub>3</sub> leaves = 33%; C<sub>3</sub> seeds = 75%; C<sub>4</sub> leaves = 25%; C<sub>4</sub> seeds = 75%; insects = 77%. Thus the potential energetic gain of food type *j* is (*K*\* $\epsilon$ \**g*), where *g* is the energetic content for each food type, and *K* varies stochastically (Karasov 1990).

We consider an interval of length *T* during which only foraging decisions influence fitness. Fitness (*W*) at the terminal time *T* is assumed to be an increasing function of *x* and  $\theta$  determined by the general function  $W(x,\theta,t=T) = \Psi(x,\theta)$ , such that an organism with maximal endogenous and exogenous energetic storage has maximum fitness. By scaling the terminal fitness function to be unity, it becomes survival after *T* for an individual whose end state is X(T) = x,  $\Theta(T) = \theta$ . The fitness function for both the terminal time, and periods prior to the terminal time is shown in Fig. 25, where maximization over *j* chooses the food that maximizes fitness given the endogenous (*x*) and exogenous ( $\theta$ ) energetic state. As the fitness function is solved from *t*<*T* to *t*=1, we obtain the decision array  $D(x,\theta,t \mid \pi)$ , which denotes the optimal foraging decision at time *t*, with X(t) = x and  $\Theta(t) = \theta$ , given a set of parameter values  $\pi$ . Moreover, we can determine which allocation strategy (cache or consume) maximizes fitness for a particular food type.

Environmentally-controlled resource distributions are important to determining which foraging strategies maximize fitness across consumer energetic states. The fitness of a consumer with a given energetic state at a given time in the season is important because it is, by definition, proportional to reproductive output, such that the probability of reproduction  $pr(x, \theta, t|M) \propto W(x, \theta, t|M)$ . This relationship allows us to assess the effects of changing environmental conditions on consumer population growth, which is determined by the difference equation  $N(t+1) = N(t) + p_r(x, \theta, t)N(x, \theta, t) - p_{\mu}(m, v)N(t)$ , where  $p_r$  is the probability distribution describing reproduction over the energetic states of individuals within the population  $N(x, \theta, t)$  (defined by the vectors x and  $\theta$ ). Linking environmental change to population dynamics will allow us to (1) validate SDP against long-term estimates of small mammal and arthropod population size and (2) predict extinction risk under forecasted changes in climate mean and variance.

Consumer SDP preliminary results. Our proof-of-concept model reproduces some qualitative trends observed in SEV data. First, the decision arrays over the course of a 100-day season for an exemplary rodent (*D. merriami*) reveal a stronger dependence on C<sub>3</sub> resources in the winter/spring (Point A, Fig. 26) and on C<sub>4</sub> resources during the monsoon, agreeing with our isotope-based dietary data (*not shown*). Because resource selection is state-dependent, high-energy foods, such as insects and C<sub>3</sub> seeds, are selected if endogenous resources are near the critical value  $x_c$  (Point B in Fig. 26), while more abundant, lower quality foods (C<sub>3</sub> vegetation in the winter/spring or C<sub>4</sub> seeds in the monsoon) are selected if



Fig. 26. Decision array  $D(x,\theta,t)$  for three time periods within a winter/spring (top panels) and summer monsoon (bottom) season. Colors denote fitness-maximizing foods listed in Fig. 25. See text for points A, B, and C.

endogenous resources are high. Moreover, in the late spring, consuming cached resources is a fitnessmaximizing strategy if such resources are available, and is increasingly utilized towards the end of the season (Point C, Fig. 26). Finally, the decision to cache foods is realized only if the endogenous energy stores of an individual are high. We note that the detailed results of our model predictions will change as we add refinements and extensions. However these initial results show that the basic framework provides new insights into seasonal resource selection, which generally agree with long-term data showing strong correlations between small mammal abundance and C<sub>3</sub> biomass (Fig. 9). Our SDP will also enable us to model the energetic and population costs associated with decreased availability of C<sub>3</sub> biomass in a drier and more variable climate predicted for the SEV over the next century.

Parameter sensitivity and fitting models to data. Foraging behaviors may be more sensitive to changes in some environmental conditions than others. Knowing this not only allows us to understand potential limitations of our model, but also can uncover important ecological insights. For example, if small changes to resource dispersion ( $\xi$ ) produce large changes in sensitivity ( $\Delta D$ ), we know that our model will demand greater accuracy in parameterizing dispersion and that changes in resource patchiness may have atypically large impacts on consumer foraging behaviors. We quantify this sensitivity as  $\Delta D = \sum x_{,\theta,t} [D(x,\theta,t \mid \pi + \xi) - D(x,\theta,t \mid \pi)]^2$  such that larger values indicate greater sensitivity to changes in the parameter set  $\pi$ . Systematically determining to what extent model results are most sensitive to parameter uncertainty/variability will yield a more robust framework for investigating the impact of environmental change on consumer populations.

Despite the detailed empirical data that we will use to parameterize many aspect of the SDP, some parameters, such as mortality from predation, will be difficult to quantify a *priori*. If unknown or less certain parameters strongly affect model results (as determined by  $\Delta D$ ), we will use current population trajectories and diet information from isotope data to find maximum-likelihood estimates by iteratively solving fitness-maximizing foraging behaviors over different values of unknown parameters, running simulations of populations forward through time, and calculating a likelihood from model output against the expected values gathered from observational data.

*Forecasting with SDP.* A primary motivation of our approach is to incorporate predicted changes in climate and biome transitions to understand consumer dynamics. As such, fitness-maximizing foraging decisions will be re-calculated for each year, with resource distributions changing as a function of climate scenarios. Integrating sequential coupling of yearly resource distributions along with transition uncertainty will allow us to assess how dietary choices, and their resulting effects on population dynamics, respond to such changes. Moreover, understanding how increasingly stressful conditions affect consumers that vary in trait conservatism is of general interest, as this information can be used to expand species distribution models, which generally do not account for dynamics dependent on physiological state.

#### Synthesis

Intellectual Merit. Proposed activities will advance the frontiers of ecology by developing and testing new theory on the ecological consequences of climate variance. Our original conceptual framework will provide a unified, process-based understanding of dryland ecological responses to climate over multiple spatial, temporal, and biological scales. We will build an exceptional platform not only to explain why drylands have changed historically, but also to predict how their structure and function will change in the coming decades. Our integrated program combines existing long-term data, current and new field experiments, and a novel quantitative modeling framework to test core ecological questions in dryland biomes (Table 4). By combining an innovative cross-biome experiment with existing long-term data across five major biomes in the Southwestern US, the SEV is poised to address critical, but unresolved, questions on the effects of climate variance — questions that can only be answered with long-term research. Among these, we will provide the first comprehensive test of the interactive effects of climate mean and variance in any ecosystem. In addition, we will develop and link three original models that simulate dryland processes at population, community, and ecosystem scales. We will expand the reach of LTER by coupling genetic and evolutionary processes to population dynamics of foundation plants and their consumers, ecosystem processes, and trajectories of ecotones. Our focus on biome transitions puts the effort where the action is for dryland ecosystems because these state transitions will have outsized impacts on ecosystem function and services.

The diversity of SEV ecotones provides a unique opportunity for comparative study of the causes and consequences of dryland biome transitions under climate change, which we will leverage to foster new LTER cross-site collaboration around the theme of climate variance. SEV LTER will continue to contribute to cross-site activities and syntheses, including ongoing involvement in several international networks (e.g., NutNet, DroughtNet, Ameriflux). In addition, SEV scientists will continue our substantial contributions to the leadership and management of the LTER Network.

RESEARCH ACTIVITY	Q1: Biome Transitions	Q2: Mechanisms of Climate Sensitivity	Q3: Biogeochemical and Biophysical Processes	Q4: Consumer Fitness and Dynamics	Q5: Biome- specific Disturbance
I. Mean - Variance Experiment	Х	Х	X		Х
II. LTER Observations: Core Data	Х	Х	Х	Х	Х
Flux Towers	Х		Х		Х
New Remote Sensing	Х				Х
New Biogeochemistry			Х		Х
III. Traits, Diversity, and Evolution		Х	Х	Х	
IV. Foundation Species Removal	Х		Х		
V. Disturbances: Abiotic & Biotic			Х		Х
VI. Modeling Framework: WAVE	Х		Х		Х
TECO		Х	Х		Х
SDP				Х	Х

Table 4. Map of planned activities to address Research Questions for the SEV site.

**Broader Impacts.** Our on-going and proposed Education and Outreach activities (next section) include mentorship and training at all levels of learning. We will build new research infrastructure, new publically available data packages, and maintain our strong ties land management through partnerships with Sevilleta NWR (USFWS), USFS, Army Corps of Engineers, and state/local agencies (Finch, Ford, Friggens, Granillo). SEV education and outreach programs will continue to reach a large number of students in Native American and Hispanic communities.

#### **Education and Outreach**

#### New Initiatives.

Interdisciplinary Distributed Graduate Seminars will focus on novel model development and cross-site syntheses of dryland dynamics and climate sensitivity functions (Rudgers, Lippitt, Miller, D'Odorico, Fuentes, Yeakel). We will jointly run a seminar in alternate years. For example, the first focus will be developing theory and analyses on the ecological effects of climate variance, using D'Odorico's book as a starting place (Ridolfi et al. 2011).

Course-based Undergraduate Research Experiences (CURE, National Academies) will integrate

SEV research into inquiry-based teachable units for BIOL 203, serving ~400 students/yr at a majorityminority institution with 44% Hispanic and 6% Native American students (Rudgers, Whitney, Newsome). We will leverage a Title V-funded course redesign effort, supported externally by the UNM STEM Gateway program. Units will include e.g., SEV ecosystem ecology, which allows students to explore and understand our flux tower data (NEE, GPP, R<sub>E</sub>); drivers of biodiversity, where students work with arthropod specimens and long-term data across SEV sites; and competition dynamics, where students compete SEV soil fungi in the lab to generate new data and learn Lotka-Volterra competition models.

SEV Data Analysis Training Course will apply cutting edge statistical tools to our long-term datasets (piloted Fall 2015, Rudgers, Collins, Miller). This course is designed for graduate students and advanced undergraduates who wish to gain greater experience with hands-on data analysis in biology. The inquirybased course features student-led projects (individual or small teams) in partnership with Sevilleta LTER Pls. Students apply data analysis tools to existing datasets in order to address novel questions about long-term ecological patterns and processes. Statistical approaches taught during the semester are tailored to the student teams, but may include community composition (ordination, NMS, PERMANOVA, rarefaction, indicator species analysis), species distribution modeling (moving habitat models), structural equation models (multi-group SEM), model selection procedures, time series analysis (wavelet) and forecasting, and network analyses. *Student Learning Objectives*: By the end of this course, students will be able to: (1) generate new questions for existing long-term, ecological datasets, (2) perform quality control and quality assurance methods on large datasets, (3) prepare datasets for Information Management, (4) understand when to apply different statistical approaches to long-term data, (5) apply at least one statistical method at the level of an expert, and (6) contribute to a written manuscript in the format of a scientific journal article.

#### **Ongoing Programming.**

SEV Schoolyard LTER Program (BEMP: Eichhorst, Shaw, since 1999) engages K-12 and college students in citizen science, where their research informs multi-million dollar natural resource management decisions (Eichhorst et al. 2012). BEMP's mission of science, education, and stewardship through long-term, hands-on student research annually involves **10,000** people, including **>3,000** K-12 students that participate in monthly field research that monitors ecological responses to climate, fire, drought, and human impacts. BEMP's annual budget leverages **~\$25 of external funding for every LTER dollar**, including grants from the US Army Corps of Engineers, Bureau of Reclamation, Environmental Protection Agency, state and local government as well as private foundations. BEMP's goal is two-fold: to deliver field-based science consistent with national science education reform efforts and to provide natural resource managers with accurate and timely analysis of ecological data, as well as monitoring and reporting on critical thresholds. BEMP staff are in the field with students and then in their classrooms as students analyze results. Most BEMP funding derives from contracts with natural resource agencies to provide deliverables of SEV research.

The majority of BEMP students are from underrepresented groups, including 55% Hispanic and 11% Native American. Many of BEMP's educational materials are bilingual (Spanish/English). Since 2014, BEMP (in partnership with Luquillo LTER) hosts a formal student webinar in Spanish for students to share their research. BEMP's internal assessment shows that 70% of BEMP students who worked for the program as either high school or college interns are now either in a STEM career or discipline in college. BEMP staff and funding concentrate on engaging students with repeated, multiple contact-hour field experiences and follow up classroom and lab work. Hundreds of BEMP participants converge annually for a series of BEMP student symposia. BEMP educational materials support Common Core non-fiction reading goals (Shaw 2010, Shaw 2013). Teachers reported that BEMP put their students into the field with a reasonable level of academic challenge and support (Shaw et al. 2005). That support includes use of UNM undergraduate and graduate biology students for quality control support and mentoring. UNM BIOL 408/508 students also contribute to K-12 classrooms by writing Data Nuggets, which consolidate SEV long-term datasets into accessible, understandable nuggets for younger students.

Partnership with the Southwestern Indian Polytechnic Institute. We have partnered Dr. Schaedla to further professional training and research opportunities for Native American students through the Geographic Information Technology (GIT) and Natural Resources Programs at the Southwest Indian Polytechnic Institute (SIPI) located in Albuquerque. Additional partners include Kiksapa Consulting, LLC, a native owned and operated scientific and technological consulting group (Mandan, ND), the USGS

EROS Data Center, and NEON. The <u>overarching objective</u> of this partnership is to enhance training of *Tribal Students and Professionals to better prepare this underrepresented group for the ecological, environmental sciences, and natural resource management workforce.* The plan includes providing "Mentor RAs" from UNM to assist with GIT classes at SIPI, and to help mentor Native students in summer research projects as part of the SEV REU Program. Big data and land-use analysis workshops at NEON will also be included for students.

SEV REU Site. Our current program (Swann, Collins) brings 10-16 undergraduates each year to conduct summer research with SEV LTER scientists (<u>5 yr stats</u>: 62% under-represented, 16% Native American, 70% female, 70% retained in STEM). Students participate in a weekly seminar series, journal club, professional development workshops, ethics training, and fieldtrips. All present their results at our annual symposium. The program includes faculty in ecology, geosciences, meteorology and fine arts to foster interdisciplinary interactions and generate new ideas. We target participation by underrepresented minorities pursuing careers in ecology. Our program exposes students to large-scale, multidisciplinary research and prepares them for the rigors of graduate school, professional careers, and responsible citizenship, exemplifying integration of research and education.

Sevilleta Visitors Center and Seminar Series. The Sevilleta National Wildlife Refuge (SNWR) constructed a new visitor center (2015) to educate the public about the role of National Wildlife Refuges, the SNWR and its environment, and the role of research in understanding and managing these ecosystems. SEV LTER scientists are actively involved with creation of educational materials, including specific exhibits highlighting LTER research. As part of this enhanced outreach, the SNWR is offering more frequent public tours and a monthly seminar series for the public. SEV faculty, graduate students and staff frequently lead refuge tours and are active, regular participants in the seminar series.

*Ecological Society of America: Strategies for Ecology, Education, Development, and Sustainability (SEEDS).* The SEV SEEDS chapter (est. 2005 by Collins) has a long and active history with the ESA, hosting both the Annual SEEDS Workshop (2005) and SEEDS Leadership workshop (2008). We will continue to work closely with SEEDS, by hosting workshops and field trips, leading regional activities, and mentoring SEEDS students.

#### **Results of Prior Support**

*Litvak, Rudgers* (LTER, \$3,920,000, 2015-18) "Long Term Pulse Dynamics in an Aridland Ecosystem." *Intellectual Merit:* Research has produced 31 publications on dryland population, community, and ecosystem responses to precipitation pulses as well as publically available datasets via SEV's LTER website. *Broader Impacts:* In addition to our Schoolyard program (described in detail above), we have trained 12 graduate students, 10 undergrads, 2 REUs per year, and supported 10 staff scientists. We also taught a new course: BIOL 502: SEV Data Analysis.

*Luo* (DBI 0850290, \$1,079,454, 2009-13) "Development of a Data Assimilation (DA) Capability Towards Ecological Forecasting in a Data-Rich Era." *Intellectual Merit*: Research has resulted in development, application, and outreach of DA techniques in ecology to improve models by parameter estimation and uncertainty analysis, producing >33 papers on DA. *Broader Impacts* include support for > 500 scientists to participate in 12 conferences, symposia, and workshops; training of graduate students and post-docs; making the methods and examples publically available.

*Miller* (DEB-1543651, \$257,724, 2015-17) "EAGER: Effects of Environmental Variability on Population Dynamics in the Long-Term Ecological Research Network." *Intellectual Merit:* This project is synthesizing population time series data from the LTER network to quantify the effects of climatic variability on population dynamics. *Broader Impacts*: The project employs one postdoc and one scientific programmer, and has supported two publications to date (Compagnoni et al. 2016, Elderd & Miller 2016).

**Newsome** (DEB-1120760/1343015, \$380,000, 2011-15) "Collaborative Research: Extending the Potential for Hydrogen Isotope Tracers in Ecology: Experiments, Biochemistry and Field studies." *Intellectual Merit*: This project developed new analytical tools to further refine use of hydrogen isotopes as tracers of food and water in consumers. Research has produced ~10 publications with 5 more in preparation or in review. *Broader Impacts*: Trained 2 graduate and 6 undergraduate students, 2 honors theses, and 5 technicians.

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