

# UNDERSTANDING PAST, CONTEMPORARY, AND FUTURE DYNAMICS OF PLANTS, POPULATIONS, AND COMMUNITIES USING SONORAN DESERT WINTER ANNUALS<sup>1</sup>

TRAVIS E. HUXMAN<sup>2,3,7</sup>, SARAH KIMBALL<sup>2,3</sup>, AMY L. ANGERT<sup>4</sup>, JENNIFER R. GREMER<sup>5</sup>,  
GREG A. BARRON-GAFFORD<sup>6</sup>, AND D. LAWRENCE VENABLE<sup>5</sup>

<sup>2</sup>Ecology and Evolutionary Biology, University of California, Irvine 92697-2525 USA; <sup>3</sup>Center for Environmental Biology, University of California, Irvine 92697-2525 USA; <sup>4</sup>Botany and Zoology, University of British Columbia, Vancouver, British Columbia, Canada, V6T 1Z4; <sup>5</sup>Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA; and <sup>6</sup>UA Biosphere 2, University of Arizona, Tucson, Arizona 85721 USA

Global change requires plant ecologists to predict future states of biological diversity to aid the management of natural communities, thus introducing a number of significant challenges. One major challenge is considering how the many interacting features of biological systems, including ecophysiological processes, plant life histories, and species interactions, relate to performance in the face of a changing environment. We have employed a functional trait approach to understand the individual, population, and community dynamics of a model system of Sonoran Desert winter annual plants. We have used a comprehensive approach that connects physiological ecology and comparative biology to population and community dynamics, while emphasizing both ecological and evolutionary processes. This approach has led to a fairly robust understanding of past and contemporary dynamics in response to changes in climate. In this community, there is striking variation in physiological and demographic responses to both precipitation and temperature that is described by a trade-off between water-use efficiency (WUE) and relative growth rate (RGR). This community-wide trade-off predicts both the demographic and life history variation that contribute to species coexistence. Our framework has provided a mechanistic explanation to the recent warming, drying, and climate variability that has driven a surprising shift in these communities: cold-adapted species with more buffered population dynamics have increased in relative abundance. These types of comprehensive approaches that acknowledge the hierarchical nature of biology may be especially useful in aiding prediction. The emerging, novel and nonstationary climate constrains our use of simplistic statistical representations of past plant behavior in predicting the future, without understanding the mechanistic basis of change.

**Key words:** desert annual plants; functional traits; global change; growth rate; photosynthesis; species coexistence; water-use efficiency.

Anthropogenic factors are changing the nature of Earth's terrestrial biosphere (IPCC, 2007). Plant ecological and evolutionary dynamics are responding, or may potentially respond, in ways that impact biodiversity, along with ecosystem goods and services (Ryan et al., 2008). Global change challenges ecological researchers to predict the future states of natural plant communities sufficiently to enable analyses of impending undesirable change (Grierson et al., 2011). Ecologists are interested not only in assessing the future of biodiversity, but also in how biological systems may feedback on the climate system. This prediction challenge connects basic, curiosity-driven ecological and evolutionary research to applied sustainability issues that require a robust understanding of biology (Clark, 2007).

There are many examples of contemporary plant and community responses to climate change (Ryan et al., 2008). For example, in the southwestern United States, future climate forecasts include warmer temperatures and increased drought, primarily through reductions in winter precipitation (IPCC, 2007). Many researchers have identified either a signature of this change already occurring (Weiss and Overpeck, 2005; McAfee and Russell, 2008) or aspects of current climate that approximate the predicted "new normal" (Overpeck and Udall, 2010). Ecological responses have been well documented as a result of this climate shift, including earlier flowering time (Crimmins et al., 2009), upslope species migration on mountain fronts (Kelly and Goulden, 2008), accelerated nonnative species expansion (Bradley et al., 2006), and widespread woody plant mortality (Breshears et al., 2005).

At the same time, a number of documented patterns initially appear inconsistent with predictions associated with warming and drying. Several examples include the downslope movement of some plant communities in the Sierra Nevada mountain range of North America (Lenoir et al., 2010), frost damage from climate warming in the Rocky Mountains (Inouye, 2008) and changes in the composition of desert communities favoring cold adapted species (Kimball et al., 2010). While such changes initially appear at odds with the regional climate perspective, they occur due to the interaction of multiple environmental features. Changes in rainfall and temperature combine to influence water balance and growing season features that together drive plant

<sup>1</sup>Manuscript received 3 September 2012; manuscript accepted 17 April 2013.

The authors thank the many students who have participated in this research over the last 30 years and Dr. Joseph McAuliffe for reminding us of our scientific heritage. The authors acknowledge funding from the National Science Foundation, the Phileology Foundation of Fort Worth Texas, along with Donald Bren and the Irvine Company through support for the Center for Environmental Biology.

<sup>7</sup>Author for correspondence (e-mail: thuxman@uci.edu), (949) 824-2594

establishment, performance, and competitive ability (Weltzin et al., 2003). Global change can benefit from a biological perspective that simultaneously focuses on understanding: (1) physiological responses to changes in conditions, (2) how such responses scale to affect whole plant performance, and (3) how variation in performance among species changes competitive interactions. These are the proximate processes that alter demography, shape communities, and influence long-term patterns of plant production.

For plant ecologists, tackling this research agenda highlights many complexities. First, it is impractical to widely deploy climate manipulations in all biomes of interest. Second, an overly developed research focus on any one global change feature ( $\text{CO}_2$ , temperature, precipitation) is unlikely to produce theory that captures the complex system response of plant communities adjusting to new environmental regimes. Finally, we need to challenge our mechanistic understanding of plant processes in time frames or physical settings other than those of the research system in which it was developed (Knapp et al., 2004). Comprehensive programs combining experimental, observational, and theoretical approaches to understand the roles of functional trait variation, demographic dynamics, and life-history evolution are more likely to be successful in producing general principles that predict plant community dynamics (Rees et al., 2001; Sutherland et al., 2013).

In this paper, we take a comprehensive approach to understanding the relationship between a community of plants and climate, asking fundamental questions in biology, including (1) how functional trait variation is related to life history strategy, (2) how the relationships between traits and strategies constrain the ecological dynamics that determine community composition through time, and (3) how the hierarchical nature of functional traits, population dynamics, community, and ecosystem processes influence potential change of a system in an altered climate. This approach recognizes that issues of physiological acclimation, phenotypic plasticity, and population dynamics are all important and related to biological change at different time-scales (e.g., Smith, 2011). Research illustrating the underlying mechanisms of changes in plants, populations, and communities to climate change is critical for robust prediction of future plant dynamics. A mechanistic understanding of plant-weather coupling is needed for future, novel climate conditions, as the nonstationarity of the contemporary climate (Milly et al., 2008) makes simplistic statistical-based predictions of future change unreliable, especially when built on representations of past plant behavior.

## THE SONORAN DESERT ANNUAL PLANT COMMUNITY

**Background and natural history**—Desert annual plants have been used as a powerful tool to understand the principles of adaptation to variable environments, the population dynamic functions of dispersal and dormancy, and how temporal variation may promote species coexistence (Cohen, 1966; Venable and Lawlor, 1980; Shmida and Ellner, 1984; Chesson and Huntly, 1988; Chesson and Huntly, 1989; Philippi and Seger, 1989; Venable et al., 1993; Chesson, 2000). All of these topics are important in the context of understanding climate change effects on ecological dynamics. Significant rainfall variation is a signature characteristic of the warm deserts of North America

(Frank and Inouye, 1994; Davidowitz, 2002). Desert annuals appear to be strongly influenced by climatic variation at many time scales, from diurnal patterns of microclimate, to storm-by-storm variation in weather, to interannual variation in precipitation and decadal oscillations, such as El Niño Southern and Pacific Decadal Oscillations (Cayan et al., 1999; Venable and Pake, 1999; Bowers, 2005; Kimball et al., 2010; Angert et al., 2010; Kimball et al., 2012; Gremer et al., 2012; Barron-Gafford et al., 2013). Species responses to rainfall appear idiosyncratic, but can be broadly classified as either highly *variable* or *buffered* with respect to year-to-year environmental variation (Venable, 2007). All species, in part, use persistent seed banks as an important strategy to mitigate risk, but the *variable* species use this feature to a greater extent—they also have higher *per capita* fecundity in very wet years and substantially lower performance during dry years (high demographic variability—geometric standard deviation of fitness over time; Venable, 2007). In contrast, the more demographically *buffered* species are present in most years, have less variable reproductive success, but make up a smaller fraction of the community in wet vs. dry years. The simple life cycles and rapid responses to environmental variation make desert annual plants a great experimental model system for understanding climate change impacts on plant communities (Patten, 1975; Venable and Pake, 1999; Venable, 2007).

**Contemporary trends in community dynamics**—We have used long-term ecological data to investigate the response of biotic communities to global climate change. Since 1982, we have followed the population dynamics of the winter annual plant species at the University of Arizona's Desert Laboratory at Tumamoc Hill (Venable and Pake, 1999; Venable, 2007). Our study site is a gently sloping alluvial plain dominated by *Larrea tridentata* (creosote bush) that has been protected from grazing since 1906. We have 72 permanent plots in the shrub-open space matrix along a 250-m transect. Plots have been visited following each winter rainfall event to map individual plants at germination and to identify species. Subsequent surveys have been conducted at biweekly to monthly intervals to monitor performance and seed production until the end of the winter growing season, which is usually in March or April. Since 1989, we have used soil cores after germination but before reproduction to determine the number of viable seeds of each species that remain in the seed bank. The soil cores are used to estimate seed densities and germination fractions (Pake and Venable, 1996). As a result of this monitoring, we have a long-term data set with the number of seedlings, the germination fraction, *per capita* survivorship (the proportion of germinated seedlings that survived to reproduce), and *per capita* fecundity (the average number of seeds produced by each plant that reproduced). We calculate *per germinant* fecundity as *per capita* survivorship multiplied by *per capita* fecundity (Venable and Pake, 1999; Venable, 2007).

Over the last 25 yr, the Sonoran Desert has been getting warmer and drier (Weiss and Overpeck, 2005). Climate models predict that this trend will continue and that the southwestern United States will be affected more by climate change than other parts of the United States (McAfee and Russell, 2008). Our weather data indicates that precipitation during the winter growing season has decreased an average of 6.6 mm/year and mean temperatures have increased an average of 0.05°C/year since we began our long-term monitoring (Kimball et al., 2010). The result has been a negative shift in water balance whereby

germination-triggering rain events have been arriving substantially later in the year, during December rather than October. Thus, despite the warming trend, germination has been occurring during periods of significantly cooler temperatures in recent years (Fig. 1). Our long-term data set shows a significant winter annual community response to these changes in weather (Kimball et al., 2010). We found that the abundance of all winter annuals has decreased over the last 25 yr, but some species have been more affected than others (Fig. 1). The change in environmental drivers has led to a community composition shift, where the relative abundance of species in the community that are classified as buffered demographically have increased significantly over time. Interestingly, based on our assessments of the physiological performance of these species, this shift with warming and

drying has resulted in a community with a greater abundance of species that are adapted to perform in cold conditions (Kimball et al., 2010).

Interestingly, while interannual climate variability has increased, the biological response was to favor strategies that are more *buffered*. From the perspective of life history evolution, such a shift may be anticipated, but in the context of community composition, it is not clear that such a response is anticipated from the global-change literature, which has focused to a large extent on predictions that are based on single factor environmental variables. This trend allows us to explore potentially new ideas about the coupling of climate and vegetation strategies to understand past, contemporary, and future trajectories of the ecology.

#### FUNCTIONAL TRAIT VARIATION AND PLANT STRATEGIES

**Underpinnings of population dynamics**—Understanding this community shift in response to climate requires a focus on how soil water balance influences processes in this desert and the associated relationships to plant strategies. Water is a critical resource in deserts, and its availability is pulsed and irregular, resulting in episodic periods of significant biological activity (Noy Meir, 1973; Huxman et al., 2004; Schwinning et al., 2004). In the Sonoran Desert, approximately half of all precipitation occurs during the summer monsoon, from July to September, with the rest falling sporadically from October to April, driving the growing season for winter annual plants (Venable, 2007). How are these species differentially responding to the same weather patterns to achieve different demographic patterns and long-term abundance? We have focused on exploring the connection between functional traits and population dynamics by conducting detailed ecophysiological measurements on the common species of this winter annual community (Angert et al., 2007; Huxman et al., 2008). We have determined relative growth rate (RGR) for each species and allocation strategies in response to rainfall variation over different time-scales and compared them to carbon isotope ratios of leaves. Isotope ratios can be a good proxy for integrated, intrinsic water-use efficiency (WUE; Ehleringer, 1993; Dawson et al., 2002). These measurements revealed that the species in this community exhibit a trade-off between growth rate and water-use efficiency (Fig. 2). Furthermore, the position along this RGR–WUE trade-off correlates with variance in *per germinant* fecundity from the long-term data collection such that *variable* species are fast-growing and have low WUE (Angert et al., 2007; Huxman et al., 2008). The opposite is true for demographically *buffered* species—they are slow-growing and have high WUE. This result has helped us understand historic linkages between individual species and population response. However, to understand contemporary trends in community structure, we must understand the determinants of growth rate and water-use.

The RGR–WUE trade-off occurs in part due to the physiological determinants of photosynthesis (Huxman et al., 2008) and to morphological strategies relating to how new leaf growth follows large rain pulses (Angert et al., 2007). The demographically variable, fast-growing species plastically produce large amounts of leaf material following large rain pulses late in the season (termed “morphological responders” by Angert et al., 2007), while the demographically buffered, slow-growing species are constrained in their growth response (termed “physiological responders”).

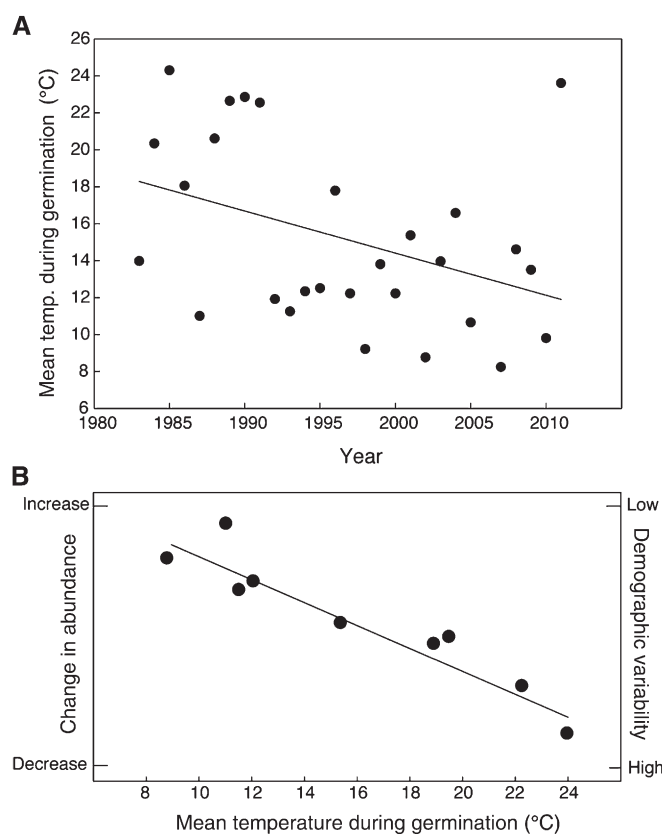


Fig. 1. The winter annual growing season begins with the first germination-triggering rain event between October and January. Over the last 35 yr, there has been a delay in the arrival of that rain event, leading to a decrease in average temperatures during germination (average daily temperature during rain and for 5 d after the rain event for each year). In (A), dots indicate each year of our study, and the line is a linear regression indicating the decrease in germination temperature over time. In (B), dots indicate the study species in our community. Species that increased in abundance or stayed the same over a 30-yr period were the ones that have historically germinated at lower temperatures. This change in the performance of different species occurred in part due to the reduction in the temperature associated with periods favoring germination (when rainfall occurred) during the fall and winter. The species that germinate under colder temperatures and have increased in abundance through time are the demographically buffered species, while those that have decreased in abundance are the demographically variable species (redrawn from Kimball et al., 2010 with additional data).



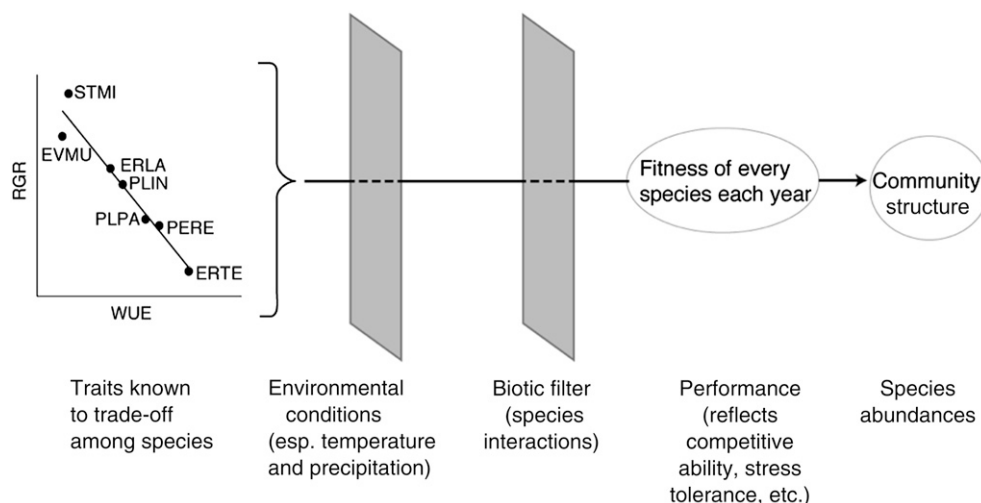


Fig. 2. Conceptual framework for understanding how environmental variation is translated into community dynamics through functional trait differences among species in the Sonoran Desert Annual plant guild. Trade-offs among traits such as relative growth rate (RGR) and water-use efficiency (WUE) could scale up to trade-offs in performance based on competitive abilities and environmental conditions. This higher-level trade-off influences germination, survival, and fecundity and determines community structure. The trade-off between RGR and WUE represents data from Huxman et al. (2008) where STMI = *Stylocline micropoides*, EVMU = *Evax multicaulis*, ERLA = *Eriophyllum lanosum*, PLIN = *Plantago insularis*, PLPA = *Plantago patagonica*, and ERTE = *Erodium texanum*.

We dissected how WUE is attained in these winter annual plants. Instantaneous WUE is the ratio of the rate of carbon assimilation through photosynthesis to the rate of water lost through stomata, and it is usually correlated with integrated WUE as measured with carbon isotope analyses (Ehleringer, 1993). Somewhat surprisingly, our measure of integrated WUE did not correlate with instantaneous measures of stomatal conductance to water vapor (and thus, the typical controlling feature of water loss). Instead, water-use-efficient species tended to have high photosynthetic rates (Huxman et al., 2008). In these species, the net photosynthetic rates in high-WUE plants appear to be due to greater proportional nitrogen allocation to the processes of light harvesting and electron transport for use in the Calvin cycle and the levels of enzymes used to initially fix  $\text{CO}_2$ . Such differential investment in photosynthetic determinants is illustrated by the relationship between  $J_{\text{max}}$  (light-saturated rate of electron transport) and  $V_{\text{Cmax}}$  (maximum rate of carboxylation, both calculated from  $\text{CO}_2$  response curves to understand the biochemistry of photosynthesis). We discovered that demographically buffered species with high WUE had consistently greater ratios of  $J_{\text{max}}$  to  $V_{\text{Cmax}}$  than our variable species and were also higher than a range of previously studied angiosperms (Wullschlegel, 1993).

It initially appears paradoxical that plants in the high light environment of a desert would have unusually high allocation to photosynthetic light capturing machinery. However, the enzymes involved in light capture are quite temperature sensitive, suggesting that this unusually high allocation may be an adaptation to increase photosynthetic carbon gain at low temperatures (Harley et al., 1992; Gremer et al., 2012). These patterns make sense considering that winter annuals escape the most water-stressed conditions of the desert by completing their life cycle during the coldest months of the year. Winter annuals are characteristic of warm, but not cold deserts (Comstock and Ehleringer, 1992), suggesting that low temperature provides a severe challenge to this life history, and provides a physiological context for the observed RGR–WUE trade-off (Fig. 3).

The more water-use efficient, buffered species appear to be especially specialized to low-temperature vs. high-temperature photosynthetic performance (Fig. 4; Gremer et al., 2012). These patterns of resource acquisition and growth may underlie differences in the phenology of their annual growth cycle, where buffered and variable species appear to be exploiting different components of the season (Huxman et al., 2008; Kimball et al., 2011).

The trait construction associated with the RGR–WUE trade-off has some interesting consequences for plant function. These species exhibit plastic responses that cause some complexity in relating traits to past dynamics. The ability of the morphological responder strategy to take advantage of late season performance during high resource years (Angert et al., 2010) means that small-scale weather is more important than “wet vs. dry” contrasts interannually. A single, large rainfall event midway through the growing season can greatly affect species rank performance. In addition, some of the species we term physiological responders have striking abilities to acclimate their metabolism to temperature throughout a growing season which can influence carbon accumulation through the balance of the photosynthetic and respiratory response (Fig. 5, Barron-Gafford, et al., 2013; Gremer et al., 2012). Thus, variation in temperature, early in the growing season, is likely to profoundly affect the carbon balance of leaves of the buffered species.

The documented RGR–WUE trade-off has been powerful in helping us understand year-to-year dynamics of this community. Fitness consequences of these functional trait combinations depend strongly on environmental conditions. In some years with large precipitation events and low temperatures (e.g., 1983), species with traits that favor growth over WUE did relatively better, while in years with less water and higher temperatures (e.g., 2007), high-WUE species did relatively better (Fig. 6). In other years, all species did well (2005) or poorly (1999) regardless of their functional traits. Understanding which aspects of weather variation favor performance of desert winter annuals in general, and which discriminate among species with different

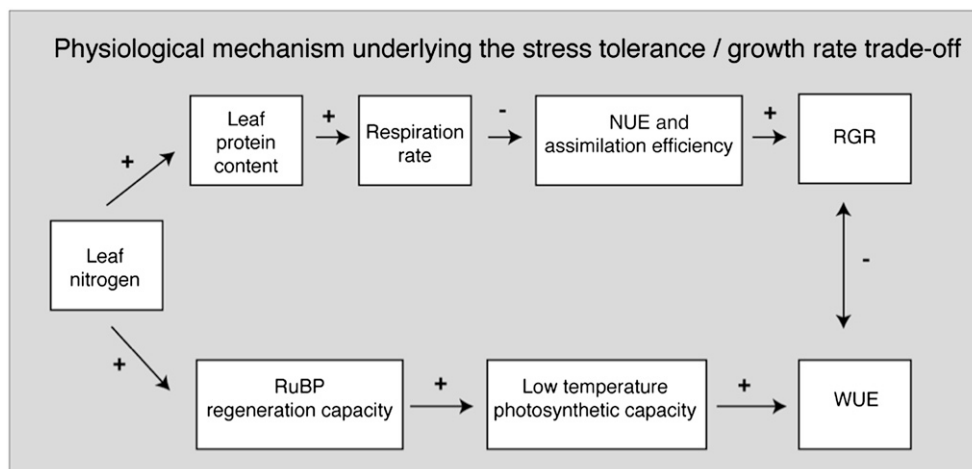


Fig. 3. The construction of the major physiological/growth strategy trade-off that strongly predicts demography for the major species in the Sonoran Desert annual plant guild (following Huxman et al., 2008). Differential patterns of leaf nitrogen allocation influence patterns of photosynthesis and respiration such that water-use efficiency and relative growth rate form an apparent trade-off. Positive and negative relationships are illustrated with symbols. NUE = nitrogen-use efficiency; RGR = relative growth rate; WUE = water-use efficiency, RuBP = ribulose 1,5 bis-phosphate.

functional traits, has been powerful in connecting our analysis of past and contemporary community dynamics, and making predictions of future change (Kimball et al., 2012).

#### TRAITS, STRATEGIES, AND COMMUNITY COMPOSITION

In contrast to understanding patterns of fecundity and demographic variability, which are predicted well from the RGR–WUE trade-off, the contemporary shift in composition through time is more complex. This change may occur through a number of processes, including changes in the germination, survival, or fecundity of species in the community (and subsequent species differences in strategies associated with each). Linear regression and hierarchical partitioning analyses of our long-term data indicated that the transition from seeds produced in the previous year to seeds germinating in the current year (seed mortality and germination), was the life history stage primarily responsible for changes in the abundance of seven of our nine focal species across years (Kimball et al., 2010). These results are a reminder that the response of biological communities through time may be influenced by many factors and the features that determine short-term fluctuations in plant growth are not necessarily the same associated with other time-scales that have implications for populations. Thus, the interrelationship of species life history strategies and organismal functional trait relationships is key to understanding the future of plant communities.

**Functional dynamics of species coexistence**—The functional and demographic differences among species have implications for how biodiversity is maintained in this system (Angert et al., 2009). Over 60 species of winter annuals have occurred in our study plots over the last 30 yr. Species diversity of germinated plants has changed from year-to-year as population sizes vary and all species do not emerge in great numbers in every year. Species richness and Shannon diversity values for seedlings are both positively related to precipitation, likely through how resource load affects the potential for high densities of all

desert annual plant species. The long-term trend of declining precipitation that influenced plant abundance was not accompanied by a long-term decline in species diversity despite the composition shifts (Venable and Kimball, in press). Rather, there has not been any major changes in diversity over the long

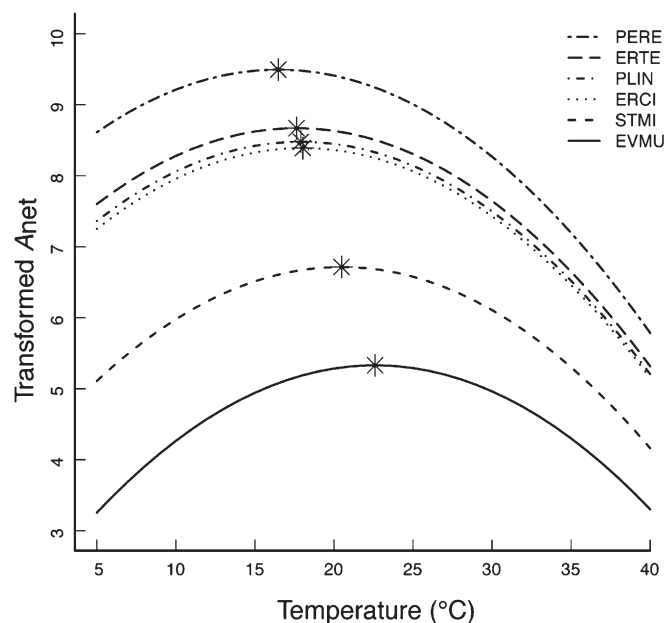


Fig. 4. Net photosynthetic rates ( $A_{\text{net}}$ ;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) averaged from measurements taken at several points in the growing season vs. temperature for six winter annual species.  $A_{\text{net}}$  values were transformed before analysis ( $A_{\text{net}}^{2/3}$ ). Lines represent temperature curves for each species (estimated using generalized linear mixed models, see Fig. 2 for species abbreviations). Asterisks represent maximum photosynthesis levels (i.e., the temperature at which species reach their optimum). High-WUE/low-RGR species (e.g., PERE and ERTE) can be seen on the upper lines and have lower temperature optima. In contrast, low-WUE/high-RGR species (e.g., EVMU and STMI) are represented by the lower lines and have higher temperature optima (data summarized from Gremer et al., 2012).

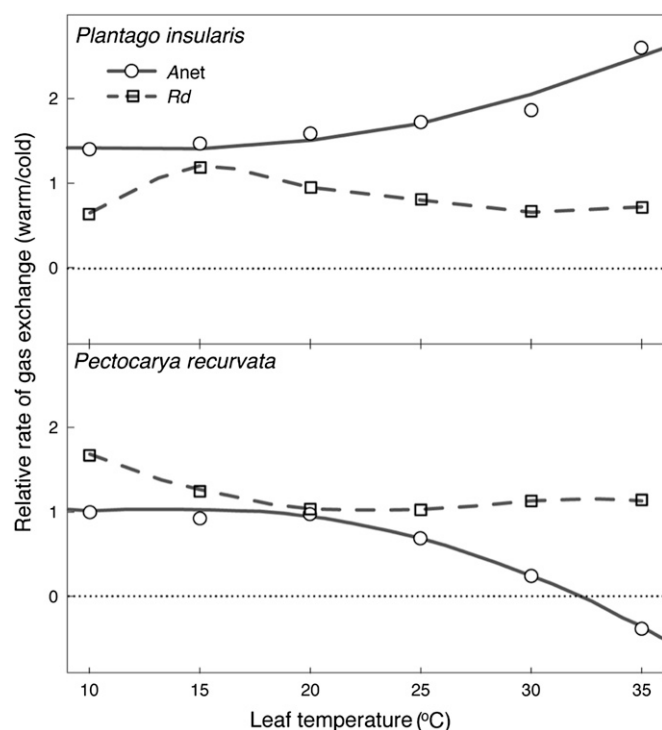


Fig. 5. Patterns of leaf level photosynthesis ( $A_{net}$ ) and respiration ( $R_d$ ) response to short-term exposure to different leaf temperatures for species acclimated to warm vs. cold treatments (redrawn and summarized from Barron-Gafford et al., 2013). *Pectocarya recurvata* (bottom panel) has a strong negative response of net photosynthesis for growth at warm vs. cold temperatures, whereas *Plantago insularis* shows increases in net photosynthesis when grown in warm conditions and exposed for short-terms to high temperatures. This occurs due to the ability of each species to acclimate both gross photosynthesis and respiration to warm vs. cold temperatures. The lack of a positive net photosynthetic response in *Pectocarya* is in part due to a greater proportional burden of respiratory loss when acclimated to high temperatures.

term (Pake and Venable, 1995; Venable, 2007). This long-term constancy in species diversity occurring alongside highly variable year-to-year population dynamics and contemporary shifts in composition suggests that strong coexistence-promoting mechanisms are at work. Given the trajectory of future climate change, it is important to understand how environmental variation and responses to that variation affect processes that influence coexistence.

Ecologists have long explored the potential mechanisms by which competing species stably coexist (Tilman and Pacala, 1993; Chesson, 2000). Some processes that focus on niche-based mechanisms for stable coexistence operate independently of environmental variation (Schoener, 1974; Tilman, 1988; Gendron, 1987), and other niche-based mechanisms that allow species to recover from low density require environmental variation for stable coexistence (Chesson, 2000, 1994; Levins and Culver, 1971; Hastings, 1980; Armstrong and McGehee, 1980; Chesson and Warner, 1981).

Sonoran Desert winter annuals are likely influenced by three coexistence-promoting mechanisms associated with environmental variability. First, a likely, but unproven (and not to be discussed here) mechanism is frequency-dependent seed predation, where high density makes the seeds of a particular species more attractive to seed predators, reducing the population growth

rate of common species and promoting species at low density. Second, resource partitioning and variability in space is certainly involved and is reflected in habitat and range differences for coexisting plants. Species differ in prevalence between bajada (fluvial piedmont or slope microsites) and flat (depositional) environments as well as in the open or under-shrub habitats (Pake and Venable, 1995). Also, the timing of life-cycle events varies by position; early germinating species germinate first in the open, while later germinating species germinate first under shrubs, and senescence also appears dependent on microhabitat (Kimball et al., 2012). All of these features are likely important for long-term species coexistence.

The third mechanism, storage effect coexistence, appears to strongly influence our system as well. The storage effect combines species-specific responses to the environment (temporal niche) and population-dynamic buffering due to persistent life history stages (such as seed banks) to generate positive average low-density growth rates for each species (Chesson, 2000). We have documented three pieces of evidence that are critical for the storage effect. First, demographic independence of species arising from partially uncorrelated responses to temporal environmental variation is a requirement and is evidenced by differences in the response of germination, survival, and fecundity to rainfall and temperature in winter annuals (Angert et al., 2009). Second, the storage effect requires some aspect of the life history providing “storage” or resistant buffering to the combined negative effects of competition and unfavorable phases of the environmental variation, and winter annuals have seed banks that allow them to persist for several years belowground (Moriuchi et al., 2000; Venable, 2007; Chesson, 1994, 2000). Finally, the degree of competition experienced by each species is assumed to covary positively with population dynamic responses to the environment to a greater extent when it is common than when it is rare—the final condition of the storage effect. When these three elements are combined, each species should have positive long-term average growth rates when at low density, resulting in stable coexistence, similar to other systems (Chesson and Warner, 1981; Caceres, 1997; Runkle, 1989; Kelly and Bowler, 2002; Adler et al., 2006; Pake and Venable, 1995). These patterns are consistent with those in winter annuals since the components of the community average storage effect, which are proportional to the species-by-time interactions for germination and for per germinant fecundity, result in increases in low-density, long-term per capita population growth rate by between 0.025 and 0.052 (Angert et al., 2009), resulting in a total low density advantage of over 10%. Given population sizes (millions of individuals of most species), any positive recovery rate is likely to be adequate to result in indefinite coexistence (Chesson and Warner, 1981; Chesson, 1994). The observed storage effect is substantial, equivalent to a doubling time of 7 yr for a species recovering from low density.

In our system, species with greater differences in functional traits and growth strategies were more decoupled in their population dynamics, i.e., these functional differences contributed to species coexistence (Angert et al., 2009). One can infer from this that the evolutionary constraint that shapes the covariance of traits through the fundamental trade-off between stress tolerance and growth rate also influences community-level diversity. How stable this relationship may be is unknown. Given the shift in weather variability within the growing season, differences in the initiation of the growth season, and changes in species composition, the coupled climate-biological system is changing significantly. How novel environmental conditions modify

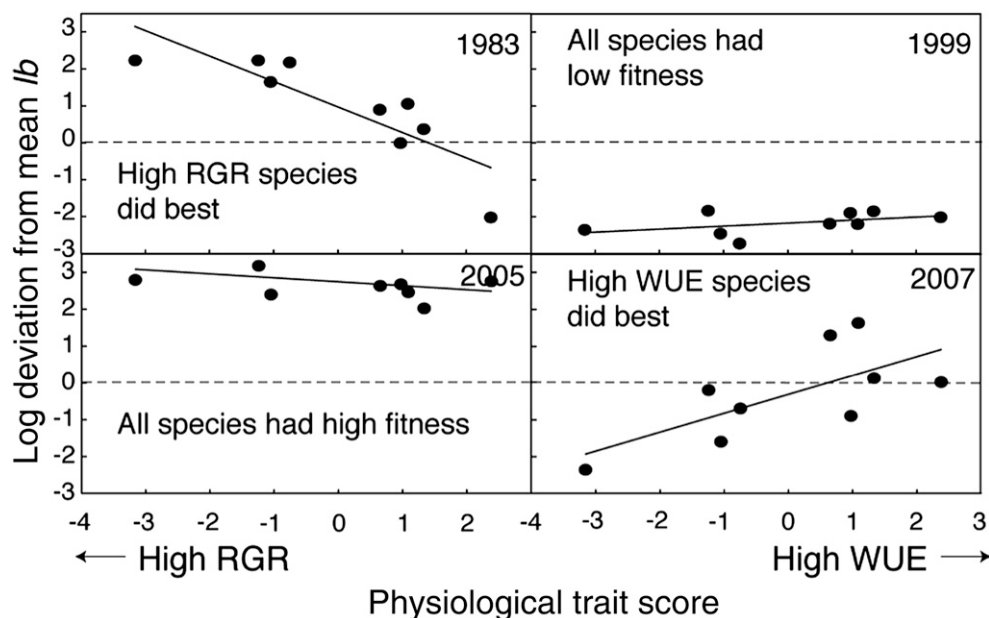


Fig. 6. Different physiological trait combinations (relative growth rate-RGR, water-use efficiency-WUE combination) result in different patterns of performance (fecundity of individuals surviving to reproduction-*lb*) across years in Sonoran Desert annual plants. The physiological trait score is a principle component score describing the major differences among the species in the traits underlying the growth rate–water use trade-off that defines our community. Years with different patterns of water and temperature covariance (cold and dry vs. warm and wet) results in different windows of opportunity for the species within seasons. Some years favor the success of stress tolerant species (2007), while some years favor the high growth rate species (1983). Some years result in relatively greater fitness for all species (2005), while some years (1999) are so low in resource availability (but may have triggered germination of all species) that no species does well relative to its long-term average fitness (rankings following Angert et al., 2007, 2010; Huxman et al., 2008, and redrawn from Kimball et al., 2010).

traits through natural selection may result in disruption of the community-wide RGR–WUE trade-off. In addition, how ecological processes change patterns of abundance over time may alter species interactions and drive different competitive pairings. Both of these issues may alter the forces that influence species coexistence. Functional trait differences among species are critical for coexistence in this system, but abiotic filtering may limit the differences left in the community as climate changes, thereby weakening coexistence. Also, the evolution of divergent phenotypes and novel ecological interactions can alter the relationship between competition and rarity in this community, impacting coexistence. An important step forward in understanding the future of biodiversity will be determining evolutionary trajectories associated with the determinants of growth rate and stress tolerance, along with how the covariation with the new climate context may alter the covariation of species, competition, and environmental variation. An additional unknown is how assembly processes, such as the insertion of nonnative species into the community pool, may impact these coexistence dynamics.

**Phenology and plant dynamics**—Many of our results point to phenological processes as being key to determining community composition. Germination is a critical early transition that may alter stress responses (Donohue et al., 2010). Germination time may alter the stage when stress is experienced, affecting the mechanism of response as well as the timing of mortality. In our system, germination variation is a strong predictor of changes in abundance (Kimball et al., 2010) and was also a large component of the storage effect (Angert et al., 2009). A better understanding of the controls over the initiation of the

growing season through germination would help in our predictions of future change. Likely the same is true for features that control the end of the growing season, such as the dynamics of senescence.

There is a rich history of plant biologists focused on the problem of understanding seed biology sufficient to describe dormancy and predict germination in natural settings. Many models have been developed (Benech-Arnold and Sanchez, 1995; Allen and Meyer, 1998; Forcella et al., 2000; Vleeshouwers and Kropff, 2000; Batlla and Benech-Arnold, 2004; Finch-Savage, 2004; Allen et al., 2007). Hydrothermal models are one successful approach that combines understanding the functional control of germination with accurate germination prediction (Bradford, 2002). Using such information to build a mechanistically based, predictive biology of germination in our system, allowing for functional understanding of germination and population and community dynamics, would help explain intriguing trait relationships among species. For example, in any given year, species with high WUE germinate and reproduce earlier in the season than species with low WUE, whereas low-WUE species have shorter reproductive phases (Kimball et al., 2011).

Another challenge is the combination of the phenological aspects of germination and the bet hedging associated with this life stage. As mentioned, bet hedging is an important process employed by plants in desert systems that likely lowers average (arithmetic mean) fitness to lower the temporal variance of fitness, thereby increasing long-term average (geometric mean) fitness (Seeger and Brockmann, 1987). There is a rich history of desert annual systems to help us understand this phenomena and to develop models to understand the evolutionary and



ecological implications (Cohen, 1966; Venable and Lawlor, 1980; Brown and Venable, 1986; Venable and Brown, 1988; Venable, 1989, 2007; Rees, 1994). The idea is that a fraction of a plant's seeds should remain dormant as a hedge against the risk of low survival and reproduction of germinating seeds. While we have gained much insight into how our functional trait and life history coupling are generally related to bet hedging, we are still working on the specific mechanisms associated with the maintenance of dormancy, which would allow us to predict important surprises, given large changes in the climatology of our system.

**Competition and change**—While germination is important in determining community composition, we also have documented a role for vegetative dynamics. The niche differences associated with growth and reproduction have been important in determining the community structure of our system and long-term species coexistence; how these niche differences translate into the forces that shape outcomes of biological interactions and their stability in the context of a changing climate would be important to know. Preliminary evidence from our system suggests that the organizing RGR–WUE trade-off affects the outcome of competition as determined by water availability, such that species with high RGR are more affected by competition at low water status, and vice versa. These patterns can promote coexistence by reducing the requirement for stabilizing effects (Chesson, 2000; Adler et al., 2006). Documenting such condition-dependent species interactions that can have strong impacts on community dynamics is a research priority (Suding et al., 2003).

Competitive interactions influence patterns of distribution and abundance that determine community structure (Grime, 1977; Tilman, 1985; Goldberg and Barton, 1992). Our most recent models for how trait differences structure coexistence in our system used relative *per capita* demographic success of species in different years to model the outcome of competitive interactions (i.e., a weighted lottery model of competition, Angert et al., 2009). This work also demonstrated a link between ecophysiological traits related to growth and these species-by-year interactions in demographic success. But from a mechanistic standpoint it is not clear how the trait combinations result in patterns of resource extraction or influence the relative performance of similar trait-value species as compared to species with significantly differences in trait values. Given that this system is shifting in the relative composition of high and low resource years, perhaps trending toward a community composed of more similar species (in terms of functional traits), understanding how more frequent competition between like-species influences community structure and the strength of the long-term coexistence forces would be desirable. At first pass, any ecological or environmental filter that reduces the differences among species would have negative effects on coexistence promoting mechanisms we know are operating in these desert annual communities.

**Extreme events and population dynamics**—Through our 30 yr of dynamical data, it is clear that low-frequency, extreme events can have important impacts on long-term dynamics. One can use the distribution of organisms across landscapes to highlight some of the ecological and evolutionary consequences of rare events (Sexton et al., 2009). These space-for-time approaches to analyze population dynamics show that the distance from the center of a species range positively relates to

variance in per germinant fecundity (Gerst et al., 2011). At the same time, there does not appear to be a relationship between the distance of our site from the center of species' ranges with mean population size or average reproductive output, suggesting that rare events and variance in vital rates are critical factors for the distribution and abundance of organisms (Olmsted et al., 1993; Bowman et al., 2005). While this insight provides us with little means to understand the directionality of the effect of rare events and variance on future community structure, it points to the importance of understanding population dynamics in addition to functional trait combinations.

Likewise, plant mortality can have an important role in controlling demography and long-term patterns of abundance. The nature of plant mortality during drought stress is a current topic of interest (Adams et al., 2009; Sala, 2009; McDowell et al., 2011). Massive mortality events in forest, chaparral, and desert systems (reviewed in McDowell et al., 2011) highlight the need to understand the interactive effects of temperature and water availability on mortality. Species are likely to differ in their susceptibility to these stresses (Condit et al., 1995; Allen and Breshears, 1998; McDowell et al., 2008), changing community structure. Deciphering variation in mortality mechanism is necessary to understand plant responses to climate change and would assist in our exploration of potential future change in the desert annual system. Plant responses may vary throughout their life cycles and between species. Stresses at early stages that restrict growth may have profound effects, but this result likely depends heavily on reproductive strategy. In our desert annual species, patterns of mortality prior to reproduction seem to vary depending on physiology. For example, one high-RGR, demographically variable species appears to have had few periods in the last 30 yr when significant mortality occurred before reproduction, but one stress-tolerant, demographically buffered species experienced frequent mortality risk prior to reproduction in each year (Fig. 7). These contrasting patterns in high-RGR and high-WUE species lead to the hypothesis that the physiology of risk aversion is closely tied to life history. Thus, we can use this system to investigate how different strategies to avoid risk may be sensitive to environmental drivers.

## THE HIERARCHICAL NATURE OF BIOLOGY AND CHANGE

Our collective results suggest that to effectively connect functional traits with demography and community structure, one needs to explicitly consider the hierarchical nature of biological processes in plant communities (Fig. 8). Such an approach, which seeks to align theory with dynamics at different spatial scales, has led to progress in connecting theory across the fields of biogeochemistry and hydrology. In particular, this approach underlies some of the recent advancement of understanding in ecohydrology (Lohse et al., 2009). How basic physiological processes, especially those associated with the physicochemical and diffusive dynamics of photosynthesis (which operate at the tissue scale), integrate into patterns of whole-plant allocation and life history strategy (which operate at the scale of the organism), provides context that bounds the potential biological response to environmental change within and between years. Our progress with desert annuals stems from understanding what type of variation was important for



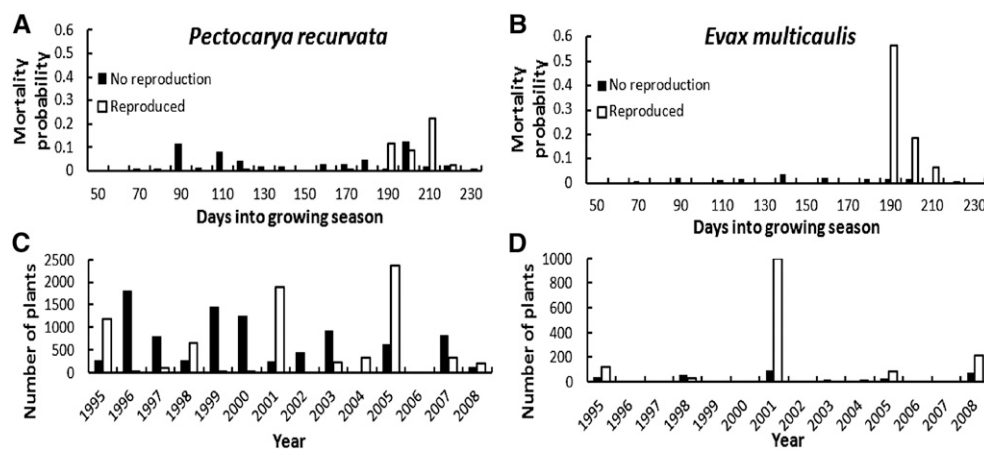


Fig. 7. Different species express different apparent strategies associated with mortality risk. Data from the long-term population censuses at Tumamoc Hill, where mortality probability either before or following first reproduction is computed from the entire 30-yr data set and set into the context of when species are actually present in high numbers. Some species germinate and attempt to establish in most years, suffering high mortality in many years, whereas other species germinate less frequently and appear to be cued into certain aspects of the environment so that they have very low probabilities of mortality given germination.

which processes at specific temporal scales. Understanding the feedbacks and relationships among life histories, physiologies, and morphological strategies is key to determining the comprehensive strategies employed by different species in this system and how the collective community may be responsive to climate. At larger scales, the structure of vegetation influences extraction rates of resources from soils and provides a biological feedback through soil biogeochemistry that constrains plant activity. Explicitly considering these feedbacks and connections among scales is important for understanding the degree to which an ecosystem may be expected to change (Lohse et al., 2009).

Forrest Shreve (1934, p. 208) best described this problem when confronting the challenges to understanding the temporal dynamics of plants in the Sonoran Desert:

“The influence of climate on physiographic and soil processes, the relationship of these to vegetation...all combine to form a vast nexus of relationships which no type of investigation dare to disregard. The problems of the desert cannot be pursued without a wide-view and a comprehensive attack.”

Understanding how environments interact with functional traits to determine population and community dynamics is a fundamental

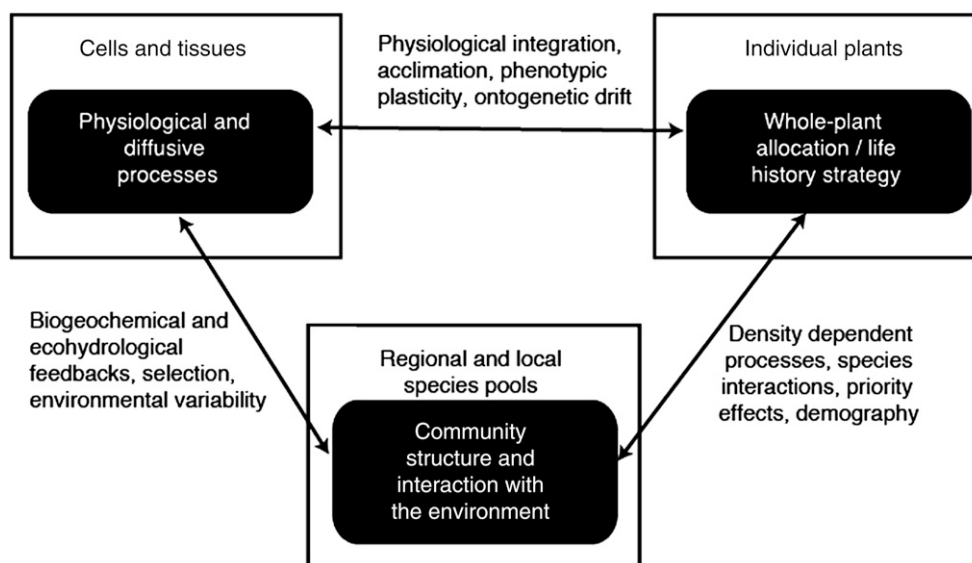


Fig. 8. The hierarchy of life creates complexities associated with predicting plant community dynamics due to the interdependences of processes at different scales. Plant ecology is fundamentally interested in processes (dark boxes) at several levels of the hierarchy of life (larger boxes), and the principles or factors that influence transitions of features between the levels (text along arrows). For example, placing trait-based assessments of function into whole-plant and intact community contexts requires an understanding of feedbacks and constraints associated with actions at different scales. Buffering processes, such as acclimation, phenotypic plasticity, bet hedging, reproductive strategy, all influence our ability to connect variation in the environment to changes in community structure through simplistic views of traits (adapted from Lohse et al., 2009).

challenge in ecology. Recent advances in linking functional biology to demographic differences (Ackerly et al., 2000; Angert et al., 2007, 2009; Huxman et al., 2008) have shown that this synthetic approach is effective for identifying the mechanisms underlying evolution of traits, interspecific interactions, mechanisms of coexistence, and community structure (Rees et al., 2001). Identifying the functional underpinnings of community dynamics is critical to predicting response to global climate change. Combining long-term studies, ecological experiments, ecophysiological studies, and theoretical modeling of Sonoran desert annuals has shown how functional traits interact with life histories to affect community change and stability, especially when evaluated within our hierarchical context (Venable et al., 1993; Pake and Venable, 1995; 1996; Venable and Pake, 1999; Angert et al., 2007; Venable, 2007; Huxman et al., 2008; Angert et al., 2009; Kimball et al., 2010, 2011; Venable and Kimball, in press).

The above results demonstrate the highly variable dynamics of desert annuals and document long-term trends attributable to warming and drying, along with the underlying mechanisms driving that change. The variability seen in these recent years is beyond the envelope we found in the 20th century. There is speculation that this is “the new normal” (Overpeck and Udall, 2010), and thus, we are presented with an interesting experiment in the coming decade—will our understanding of the system be sufficient to predict behavior in what will be transient communities? Though detailed predictions remain elusive, it seems clear that the new hydroclimatology will affect the long-term trajectory of this community and influence the ecological and evolutionary processes that are important for maintaining biological diversity.

## LITERATURE CITED

- ACKERLY, D. D., S. A. DUDLEY, S. E. SULTAN, J. SCHMITT, J. S. COLMEAN, C. R. LINDER, D. R. SANDQUIST, ET AL. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions. *Bioscience* 50: 979–995.
- ADAMS, H. D., M. GUARDIOLA-CLARAMONTE, G. BARRON-GAFFORD, J. C. VILLEGAS, D. D. BRESHEARS, C. B. ZOU, P. A. TROCH, AND T. E. HUXMAN. 2009. Warmer, global-change-type drought accelerates tree mortality. *Proceedings of the National Academy of Sciences USA* 106: 7063–7066.
- ADLER, P. B., J. HILLERISLAMBERS, P. C. KYRAKIDIS, Q. F. GUAN, AND J. M. LEVINE. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences USA* 103: 12793–12798.
- ALLEN, C. D., AND D. D. BRESHEARS. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA* 95: 14839–14942.
- ALLEN, P. S., R. L. BENECH-ARNOLD, D. BATLLA, AND K. J. BRADFORD. 2007. Modeling of seed dormancy. In K. J. Bradford and H. Nonogaki [eds.], *Seed development, dormancy and germination*, Annual Plant Reviews, vol. 27, 72–110. Blackwell, Ames, Iowa, USA.
- ALLEN, P. S., AND S. E. MEYER. 1998. Ecological aspects of seed dormancy loss. *Seed Science Research* 8: 183–191.
- ANGERT, A. L., T. E. HUXMAN, G. A. BARRON-GAFFORD, K. L. GERST, AND D. L. VENABLE. 2007. Linking growth strategies to long-term population dynamics in a guild of desert annuals. *Journal of Ecology* 95: 321–331.
- ANGERT, A. L., T. E. HUXMAN, P. CHESSON, AND D. L. VENABLE. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences USA* 106: 11641–11645.
- ANGERT, A. L., J. L. HORST, T. E. HUXMAN, AND D. L. VENABLE. 2010. Phenotypic plasticity and precipitation response in Sonoran Desert winter annuals. *American Journal of Botany* 97: 405–411.
- ARMSTRONG, R. A., AND R. McGEHEE. 1980. Competitive exclusion. *American Naturalist* 115: 151–170.
- BARRON-GAFFORD, G. A., A. L. ANGERT, D. L. VENABLE, A. P. TYLER, K. L. GERST, AND T. E. HUXMAN. 2013. Photosynthetic temperature responses of co-occurring desert winter annuals with contrasting resource-use efficiencies and different temporal patterns of resource utilization may allow for species coexistence. *Journal of Arid Environments* 91: 95–103.
- BATLLA, D., AND R. L. BENECH-ARNOLD. 2004. A predictive model for dormancy loss in *Polygonum aviculare* L. seeds based on changes in population hydrotime parameters. *Seed Science Research* 14: 277–286.
- BENECH-ARNOLD, R. L., AND R. A. SANCHEZ. 1995. Modeling weed seed germination. In J. Kigel and G. Galili [eds.], *Seed development and germination*, 545–566. Marcel Dekker, New York, New York, USA.
- BOWERS, J. E. 2005. El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts. *Journal of the Torrey Botanical Society* 132: 38–49.
- BOWMAN, J., G. L. HOLLOWAY, J. R. MALCOLM, K. R. MIDDEL, AND P. J. WILSON. 2005. Northern range boundary dynamics of southern flying squirrels: Evidence of an energetic bottleneck. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 83: 1486–1494.
- BRADFORD, K. J. 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science* 50: 248–260.
- BRADLEY, B. A., R. A. HOUGHTON, J. F. MUSTARD, AND S. P. HAMBURG. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* 12: 1815–1822.
- BRESHEARS, D. D., N. S. COBB, P. M. RICH, K. P. PRICE, C. D. ALLEN, R. G. BALICE, W. H. ROMME, ET AL. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* 102: 15144–15148.
- BROWN, J. S., AND D. L. VENABLE. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *American Naturalist* 127: 31–47.
- CACERES, C. E. 1997. Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proceedings of the National Academy of Sciences USA* 94: 9171–9175.
- CAYAN, D. R., K. T. REDMOND, AND L. G. RIDDLE. 1999. ENSO and hydrologic extremes in the western United States. *Journal of Climate* 12: 2881–2893.
- CHESSON, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45: 227–276.
- CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- CHESSON, P., AND N. HUNTLY. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology & Evolution* 4: 293–298.
- CHESSON, P. L., AND N. HUNTLY. 1988. Community consequences of life-history traits in a variable environment. *Annales Zoologici Fennici* 25: 5–16.
- CHESSON, P. L., AND R. R. WARNER. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117: 923–943.
- CLARK, W. C. 2007. Sustainability science: A room of its own. *Proceedings of the National Academy of Sciences USA* 104: 1737–1738.
- COHEN, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12: 119–129.
- COMSTOCK, J. P., AND J. R. EHRLINGER. 1992. Plant adaptation in the Great Basin and Colorado Plateau. *Great Basin Naturalist* 52: 195–215.
- CONDIT, R., S. P. HUBBELL, AND R. B. FOSTER. 1995. Mortality-rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65: 419–429.
- CRIMMINS, T. M., M. A. CRIMMINS, AND C. D. BERTELSEN. 2009. Flowering range changes across an elevation gradient in response to warming summer temperatures. *Global Change Biology* 15: 1141–1152.
- DAVIDOWITZ, G. 2002. Does precipitation variability increase from mesic to xeric biomes? *Global Ecology and Biogeography* 11: 143–154.

- DAWSON, T. E., S. MAMBELLI, A. H. PLAMBOECK, P. H. TEMPLER, AND K. P. TU. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.
- DONOHUE, K., R. R. DE CASA, L. BURGHARDT, K. KOVACH, AND C. G. WILLIS. 2010. Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* 41: 293–319.
- EHLERINGER, J. R. 1993. Gas-exchange implications of isotopic variation in arid-land plants. In J. A. C. Smith and H. Griffiths [eds.], *Water deficits: Plant responses from cell to community*, 265–284. Bios Scientific Publishers, Oxford, UK.
- FINCH-SAVAGE, W. E. 2004. The use of population-based threshold models to describe and predict the effects of seedbed environment on germination and seedling emergence of crops. In R. L. Benesh-Arnold and R. A. Sanchez [eds.], *Handbook of seed physiology: Applications to agriculture*. Food Products Press, New York, New York, USA.
- FORCELLA, F., R. L. B. ARNOLD, R. SANCHEZ, AND C. M. GHERSA. 2000. Modeling seedling emergence. *Field Crops Research* 67: 123–139.
- FRANK, D. A., AND R. S. INOUE. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems—Patterns and ecological implications. *Journal of Biogeography* 21: 401–411.
- GENDRON, R. P. 1987. Models and mechanisms of frequency-dependent predation. *American Naturalist* 130: 603–623.
- GERST, K. L., A. L. ANGERT, AND D. L. VENABLE. 2011. The effect of geographic range position on demographic variability in annual plants. *Journal of Ecology* 99: 591–599.
- GOLDBERG, D. E., AND A. M. BARTON. 1992. Patterns and consequences of interspecific competition in natural communities—A review of field experiments with plants. *American Naturalist* 139: 771–801.
- GREMER, J. R., S. KIMBALL, A. L. ANGERT, D. L. VENABLE, AND T. E. HUXMAN. 2012. Variation in photosynthetic response to temperature in a guild of winter annual plants. *Ecology* 93: 2693–2704.
- GRIERSON, C. S., S. R. BARNES, M. W. CHASE, M. CLARKE, D. GRIERSON, K. J. EDWARDS, G. J. JELLIS, ET AL. 2011. One hundred important questions facing plant science research. *New Phytologist* 192: 6–12.
- GRIME, J. P. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- HARLEY, P. C., R. B. THOMAS, J. F. REYNOLDS, AND B. R. STRAIN. 1992. Modeling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant, Cell & Environment* 15: 271–282.
- HASTINGS, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18: 363–373.
- HUXMAN, T. E., G. BARRON-GAFFORD, K. L. GERST, A. L. ANGERT, A. P. TYLER, AND D. L. VENABLE. 2008. Photosynthetic resource-use efficiency and demographic variability in desert winter annual plants. *Ecology* 89: 1554–1563.
- HUXMAN, T. E., K. A. SNYDER, D. TISSUE, A. J. LEFFLER, W. POCKMAN, K. OGLE, D. SANDQUIST, D. L. POTTS, AND S. SCHWINNING. 2004. Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia* 141: 254–268.
- INOUE, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362.
- IPCC [INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE]. 2007. *Climate Change 2007: The physical science basis*. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, H. L. Miller [eds.], Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, New York, USA.
- KELLY, A. E., AND M. L. GOULDEN. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences USA* 105: 11823–11826.
- KELLY, C. K., AND M. G. BOWLER. 2002. Coexistence and relative abundance in forest trees. *Nature* 417: 437–440.
- KIMBALL, S., A. L. ANGERT, T. E. HUXMAN, AND D. L. VENABLE. 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Global Change Biology* 16: 1555–1565.
- KIMBALL, S. A., A. L. ANGERT, T. E. HUXMAN, AND D. L. VENABLE. 2011. Differences in the timing of germination and reproduction relate to growth physiology and population dynamics of Sonoran Desert winter annuals. *American Journal of Botany* 98: 1773–1781.
- KIMBALL, S., J. R. GREMER, A. L. ANGERT, T. E. HUXMAN, AND D. L. VENABLE. 2012. Fitness and physiology in a variable environment. *Oecologia* 169: 319–329.
- KNAPP, A. K., M. D. SMITH, S. L. COLLINS, N. ZAMBATIS, M. PEEL, S. EMERY, J. WOJDAK, ET AL. 2004. Generality in ecology: Testing North American grassland rules in South African savannas. *Frontiers in Ecology and the Environment* 2: 483–491.
- LENOIR, J., J. C. GEGOUT, A. GUIAN, P. VITTOZ, T. WOHLEGMUTH, N. E. ZIMMERMANN, S. DULLINGER, ET AL. 2010. Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33: 295–303.
- LEVINS, R., AND D. CULVER. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences USA* 68: 1246–1248.
- LOHSE, K. A., P. D. BROOKS, J. C. MCINTOSH, T. MEIXNER, AND T. E. HUXMAN. 2009. Interactions between biogeochemistry and hydrologic systems. *Annual Review of Environment and Resources* 34: 65–96.
- MCAFFEE, S. A., AND J. L. RUSSELL. 2008. Northern annular mode impact on spring climate in the western United States. *Geophysical Research Letters* 35: L17701.
- MCDOWELL, N. G., D. J. BEERLINE, D. D. BRESHEARS, R. A. FISHER, K. F. RAFFA, AND M. STITT. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26: 523–532.
- MCDOWELL, N., W. T. POCKMAN, C. D. ALLEN, D. D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, ET AL. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- MILLY, P. C. D., J. BETANCOURT, M. FLAKENMARK, R. M. HIRSCH, Z. W. KUNDZEWICZ, D. P. LETTENMAIER, AND R. J. STOUFFER. 2008. Climate change—Stationarity is dead: Whither water management? *Science* 319: 573–574.
- MORIUCHI, K. S., D. L. VENABLE, C. E. PAKE, AND T. LANGE. 2000. Direct measurement of the seed bank age structure of a Sonoran Desert annual plant. *Ecology* 81: 1133–1138.
- NOY-MEIR, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- OLMSTED, I., H. DUNEVITZ, AND W. J. PLATT. 1993. Effects of freezes on tropical trees in Everglades National Park, Florida, USA. *Tropical Ecology* 34: 17–34.
- OVERPECK, J., AND B. UDALL. 2010. Dry times ahead. *Science* 328: 1642–1643.
- PAKE, C. E., AND D. L. VENABLE. 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success? *Ecology* 76: 246–261.
- PAKE, C. E., AND D. L. VENABLE. 1996. Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. *Ecology* 77: 1427–1435.
- PATTEN, D. T. 1975. Phenology and function of Sonoran Desert annuals in relation to environmental changes. USABP Desert Biome Research Memorandum 75010, 109–116. Utah State University, Logan, Utah, USA.
- PHILIPPI, T., AND J. SEGER. 1989. Hedging ones evolutionary bets, revisited. *Trends in Ecology & Evolution* 4: 41–44.
- REES, M. 1994. Delayed germination of seeds—A look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* 144: 43–64.
- REES, M., R. CONDIT, M. CRAWLEY, S. PACALA, AND D. TILMAN. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650–655.
- RUNKLE, J. R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546–547.
- RYAN, M. G., S. R. ARCHER, R. BIRDSEY, C. DAHM, L. HEATH, J. HICKE, D. HOLINGER, ET AL. 2008. Land resources: Forests and arid lands. In P. Backlund, A. Janetos, and D. Schimel [lead authors], *The effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States*, 75–120. A report by the U.S. Climate Change Science Program and the Sub-committee on Global



- Change Research, Washington D.C., USA. Available at [http://www.amwa.net/galleries/climate-change/CCSP\\_Ag\\_Report.pdf](http://www.amwa.net/galleries/climate-change/CCSP_Ag_Report.pdf).
- SALA, A. 2009. Lack of direct evidence for the carbon-starvation hypothesis to explain drought-induced mortality in trees. *Proceedings of the National Academy of Sciences USA* 106: E68.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.
- SCHWINNING, S., O. E. SALA, M. E. LOIK, AND J. R. EHLERINGER. 2004. Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141: 191–193.
- SEGER, J., AND H. J. BROCKMANN. 1987. What is bet-hedging? In P. H. Harvey and L. Partridge [eds.], *Oxford surveys in evolutionary biology*, 182–211. Oxford University Press, Oxford, UK.
- SEXTON, J. P., P. J. MCINTYRE, A. L. ANGERT, AND K. J. RICE. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics* 40: 415–436.
- SHMIDA, A., AND S. P. ELLNER. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29–55.
- SHREVE, F. 1934. The problems of the desert. *Scientific Monthly* (March): 199–209.
- SMITH, M. D. 2011. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* 99: 656–663.
- SUDING, K. N., D. E. GOLDBERG, AND K. M. HARTMAN. 2003. Relationships among species traits: Separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.
- SUTHERLAND, W. J., R. P. FRECKLETON, H. C. J. GODFRAY, S. R. BEISSINGER, T. BENTON, D. D. CAMERON, Y. CARMEL, ET AL. 2013. Identification of 100 fundamental ecological questions. *Journal of Ecology* 101: 58–67.
- TILMAN, D. 1985. The resource–ratio hypothesis of plant succession. *American Naturalist* 125: 827–852.
- TILMAN, D. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in population biology, vol. 26. Princeton University Press, Princeton, New Jersey USA.
- TILMAN, D., AND S. W. PACALA. 1993. Species coexistence mechanisms in plants. In R. E. Ricklefs and D. Schluter [eds.], *Species diversity in ecological communities*, 13–25. University of Chicago Press, Chicago, Illinois, USA.
- VENABLE, D. L. 1989. Modeling the evolutionary ecology of seed banks. In M. A. Leck, V. T. Parker, and R. L. Simpson [eds.], *The ecology of soil seed banks*, 67–87. Academic Press, San Diego, California, USA.
- VENABLE, D. L. 2007. Bet hedging in a guild of desert annuals. *Ecology* 88: 1086–1090.
- VENABLE, D. L., AND J. S. BROWN. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131: 360–384.
- VENABLE, D. L., AND S. KIMBALL. In press. Population and community dynamics of Sonoran Desert winter annuals. In C. K. Kelly, M. G. Bowler, and G. A. Fox [eds.], *Temporal dynamics and ecological process*. Cambridge University Press, Cambridge, UK.
- VENABLE, D. L., AND L. LAWLOR. 1980. Delayed germination and dispersal in desert annuals: Escape in space and time. *Oecologia* 46: 272–282.
- VENABLE, D. L., AND C. E. PAKE. 1999. Population ecology of Sonoran Desert annual plants. In R. H. Robichaux [ed.], *Ecology of Sonoran Desert plants and plant communities*, 115–142. University of Arizona Press, Tucson, Arizona, USA.
- VENABLE, D. L., C. E. PAKE, AND A. C. CAPRIO. 1993. Diversity and coexistence of Sonoran desert winter annuals. *Plant Species Biology* 8: 207–216.
- VLEESHOUWERS, L. M., AND M. J. KROPPF. 2000. Modelling field emergence patterns in arable weeds. *New Phytologist* 148: 445–457.
- WEISS, J. L., AND J. T. OVERPECK. 2005. Is the Sonoran Desert losing its cool? *Global Change Biology* 11: 2065–2077.
- WELTZIN, J. F., M. E. LOIK, S. SCHWINNING, D. G. WILLIAMS, P. FAY, B. HADDA, J. HARTE, ET AL. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53: 941–952.
- WULLSCHLEGER, S. D. 1993. Biochemical limitations to carbon assimilation in C<sub>3</sub> plants: A retrospective analysis of the A/C<sub>i</sub> curves from 109 species. *Journal of Experimental Botany* 44: 907–920.