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Research Statement

A fundamental question in ecology is how individuals, populations, and communities respond to the environment as it changes. Variation in environmental conditions can pose a significant challenge for performance, because matching the optimal phenotype to the environment can be difficult or simply impossible. On the other hand, if individuals meet the challenges of environmental variation in different ways, it can provide opportunities for different strategies to succeed, thus promoting diversity of form and function. My research seeks to identify traits that relate to performance in variable environments to understand the processes driving life history evolution, population dynamics, and community structure. By distinguishing which traits determine performance, this approach transcends taxonomic identity, allowing for generalization of patterns across systems. My research employs a variety of methods in physiology, ecology, and demography to understand these processes. Although rarely used to address questions in ecology and evolution, this integrative approach is essential for understanding the mechanisms leading to the patterns and processes that occur in nature. I use this approach to address three main research questions: 1) How does environmental variation interact with life history traits to affect fitness? 2) How does variation in physiological traits affect population and community dynamics in variable environments? and 3) How can insights from addressing questions 1 and 2 be applied to understand and manage responses to global climate change?

Life history traits and variable environments

All organisms have the same basic elements to their life cycle: birth, growth, reproduction, and death. In nature, organisms often delay one or more of these functions. Such delays have long fascinated evolutionary ecologists, because fitness-enhancing activities such as growth and reproduction are postponed. All else being equal, individuals that grow and reproduce now will have higher fitness than those that delay these activities, due to the multiplicative nature of fitness. However, life history delays can be adaptive depending on the ecological context in which they occur. My research investigates the causes and consequences of life history delays, and how the environment mediates those relationships.

For my dissertation research, I studied a poorly understood life history delay seen in herbaceous perennial plants, known as prolonged dormancy. In prolonged dormancy, a fraction of mature individuals in a population remain below ground at a time when other individuals resprout and resume growth above ground. At first glance, prolonged dormancy seems costly since dormant plants are missing opportunities for growth and reproduction. Why remain dormant while other individuals emerge? My research on a native Montana perennial, *Astragalus scaphoides,* indicates that stored resources act as a cue that integrates past environmental conditions, previous performance, and current condition to determine whether a plant goes dormant or not (Gremer et al. 2010; *Ecology*). Environmental context then mediates the consequences of remaining dormant. I showed that risking emergence and experiencing stressors such as predation and drought results in decreased flowering probabilities and even death, thus quantifying the risk that dormant plants can avoid (Gremer & Sala 2013; *Oecologia*). Finally, I used matrix models and a long-term demographic dataset to determine the fitness consequences of prolonged dormancy. This analysis revealed that prolonged dormancy can buffer individuals from the negative effects of environmental stochasticity, and that intermediate levels of dormancy confer the highest fitness advantage (Gremer et al. 2012; *The American Naturalist*). Together, this work has identified both the proximate and ultimate causes and consequences associated with prolonged dormancy and has advanced our understanding of this peculiar life history stage. My research demonstrated that, while the costs and benefits are context-dependent, prolonged dormancy can act as an adaptive strategy to minimize risk in a variable environment.

While adult plants can enter and emerge from prolonged dormancy multiple times throughout their lifetimes, seeds can only emerge from dormancy once, making germination a critical transition that will determine performance at early, and often more vulnerable, life stages. Recent and current projects ask how this early life history delay impacts performance under different conditions using both long-term observation and short-term experimentation. With Dr. Larry Venable (University of Arizona), I used a models parameterized with 30 years of field data to determine the fitness consequences of delaying germination in a variable environment (Gremer and Venable, *in review, Ecology Letters*). This empirical parameterization incorporated performance throughout the life cycle: natural field measured variation in seed survival, survival of seedlings, and fecundity all measured over 30 years. I then tested for optimality by identifying the evolutionarily stable strategies (ESSs) predicted by the model for each species and compared them to long-term patterns of germination in the field. Model predictions corresponded remarkably well with observed germination patterns, showing that plants are actually behaving as expected in the field. Because I integrated performance throughout the life cycle and tested for optimality of behavior within the relevant ecological and evolutionary context, this study represents an unusually thorough exploration of delayed germination. While this study looked exclusively at delaying germination for one or more years, selection on germination timing may also operate within years. For instance, germinating early in the season may provide a pre-emptive competitive advantage as well as ample time to acquire resources. Conversely, later germination can act to avoid exposure to potential hazards during the season, but provides less time for resource acquisition and growth. Thus, fully understanding the adaptive value of delayed germination requires understanding within-season germination phenology as well as among-year germination fractions. Currently I am working on projects that utilize both long-term monitoring data and field experiments to understand how these two types of germination timing affect fitness in a variable environment. In doing so, I seek a comprehensive understanding of the selective forces driving the evolution of germination timing in a variable environment.

Physiological traits and community dynamics

Identifying the processes that create and maintain diversity in communities is a long standing ecological problem. Most, if not all, theories for how species stably coexist require species to have ecological differences. For example, coexisting species may differ in their responses to multiple limiting resources, interactions with predators and pathogens, or responses to climatic conditions. Therefore, identifying traits that determine responses to environmental factors provides insight into factors affecting biodiversity.

My research combines short-term experiments with long-term observation to understand how variation in responses to the environment creates ecological differences that, in turn, can promote diversity. As a postdoc at University of Arizona, I focused on a community of annual plants in the Sonoran Desert that emerge in response to winter rains. This community has become a model system for linking functional biology to population and community processes, due to detailed physiological studies coupled with 30 years of demographic data for each species in the community. These winter annual species exhibit a tradeoff between growth capacity and stress tolerance, such that species with high relative-growth rate have low water-use efficiency, and vice versa. My work investigates how variation in traits that underlie this tradeoff creates differential responses to environmental conditions. I have demonstrated that differences in physiological traits lead to variation in temperature responses, which in turn affects patterns of water use among species (Gremer et al. 2012; *Ecology*). A greenhouse experiment demonstrated that these traits then affect the outcome of species interactions across water availability gradients (Gremer et al. 2013, *American Journal of Botany*). Since both temperature and precipitation are highly variable in this desert environment, such differential responses to temperature, water, and competition can provide different windows of opportunity for species to succeed. Analysis of long-term data in this system revealed that the same traits responsible for these short-term experimental responses interact with variation in growing season weather to determine long-term patterns of fitness (Kimball, Gremer, et al. 2012; *Oecologia*). Specifically, species with traits conferring high relative-growth rate are favored in years with large, frequent rain events, whereas species with traits associated with high water-use efficiency do relatively better in years with infrequent rain and warmer temperatures at the end of the season. Thus, the trait set that maximizes fitness has varied from year to year over the past three decades in response to patterns of seasonal weather, resulting in different species being favored over time. Together, this research demonstrates how functional traits can create ecological differences that promote coexistence and maintain species diversity.

While annual plants are an important component of communities, most ecosystems include both long and short-lived species. My goal is to expand this research to understand how variation in physiological traits drive population and community dynamics in longer-lived species with more complex life histories. Short-term responses to environmental conditions do not always predict longer-term patterns of growth, survival, and reproduction. This is particularly true in long-lived species that can use stored resources to buffer the effects of short-term changes in resource assimilation. Moreover, a comprehensive understanding of these processes is lacking for herbaceous perennial species, which constitute a significant source of biodiversity in many systems. As assistant professor, I will address these complexities using long term observation to identify key life stages, as well as experimentation at those critical stages. Together, my research on both short-lived species as well as those with more complex life histories will provide critical information on how physiological trait variation scales to affect community structure and evolution.

Mechanisms driving population and community responses to climate change

Climate change forecasts include a change in both the mean and variance of temperature and precipitation. Therefore, identifying the functional and demographic responses to these conditions is critical to predicting responses to global climate change. However, it has proven difficult to understand what aspects of climate are driving variation in responses. In part, this is due to the fact that differences in microclimate and soils, as well as interactions with other plants and species, can mediate responses to climate. Using long-term monitoring data collected by various researchers across four of the Southwestern deserts (Colorado Plateau, Mojave Desert, Sonoran Desert, and Chihuahuan Desert) and detailed information on climate and soils, my current research at the U.S. Geological Survey seeks a mechanistic understanding of plant responses that explicitly incorporates the influences of these factors. In particular, I am collaborating with a soil ecologist (Mike Duniway) and an ecosystem ecologist (John Bradford) to use soil water simulation models to translate changes in climate into actual differences in plant available water, the strongest limiting resource in the Desert Southwest. In addition to incorporating soil water dynamics, my research will identify traits of species, communities, and ecosystems that make them vulnerable or resilient to these changes. By doing so, I will determine how functional biology scales to drive community and ecosystem response to change, which remains a grand challenge in ecology. Furthermore, by understanding past responses to climate change, and the mechanisms driving them, I will provide decision-making tools to predict and manage natural systems confronted with change.

Significance

My research program seeks to mechanistically understand the processes driving population dynamics, patterns of diversity, and life history evolution. I use an integrative approach that links physiological traits with demographic and community processes. My research uses field experiments and demographic observations, as well as greenhouse and growth chamber studies to understand these processes. Because my work synthesizes findings across different levels of biological organization, my research is collaborative by nature and I look forward to interacting with the faculty at University of California, Davis. I believe that my approach to research provides a powerful vantage to gain new insights into ecological questions, and I will contribute to a framework that will improve our understanding of natural systems and advance efforts to predict and manage vegetation responses to a changing environment.