Preliminary Proposal: SG: Revisiting How Species Coexist to Understand the Relationship Between Ecosystem Stability and Environmental Variability

I. Personnel

Principle Investigator

Lawrence Venable (PI). Professor, Department of Ecology and Evolutionary Biology, University of Arizona. Venable is a plant population and community ecologist who will provide the focal data sets, will supervise the use of the demographic data and modeling, and will play a major role in supervising the research.

All Other Personnel

Andrew Tredennick (Postdoctoral Researcher). Postdoctoral Fellow, Department of Wildland Resources and the Ecology Center, Utah State University. Tredennick is a quantitative ecologist who will lead all aspects of the proposed work, including: developing theory, fitting dynamic population models to data, and simulating the population models to test theoretical predictions.

Jennifer Gremer (Senior Personnel). Assistant Professor, Department of Evolution and Ecology, University of California at Davis. Gremer is a quantitative population ecologist who will provide expertise with the focal data sets and associated population modeling.

II. Project Description

1. Background. Temporal environmental variation permeates through all levels of ecological systems. It can drive the evolution of traits and species, determine the viability of populations, allow species to coexist, and impact the stability of ecosystem functioning. Yet, rarely are the impacts of environmental fluctuations at one level of organization explicitly accounted for in the processes that occur at other levels. For example, despite rapid theoretical and empirical progress in the fields of species coexistence and biodiversity-ecosystem functioning (BEF) over the last 20 years, research on the two topics remains separate. Consequently, we lack a satisifactory answer to a fundamental question of applied relevance: *How will ecosystem stability respond to increasing environmental variability?*

An intuitive prediction is that ecosystem functioning will become less stable as environmental variability increases. Such a prediction stems from two lines of evidence. First, increasing environmental variability will cause species' abundances to fluctuate more through time, assuming their growth depends on some set of environmental drivers. Second, low-abundance species are more likely to go extinct as environmental variability increases. Given the well-supported positive relationship between diversity and ecosystem stability, species losses will cause ecosystems to become more variable. What this prediction ignores, however, is the impact of species additions.

Environmental variability is a doubled-edged sword: it can increase the probability of stochastic extinctions *and* it can promote species coexistence (Adler & Drake 2008).

A less intuitive prediction is that ecosystem functioning will neither increase nor decrease in stability as environmental variability increases. This prediction still assumes that species' abundances will fluctuate more as environmental variability increases, but those increases are compensated for by species additions (Tredennick et al. in review). Species additions occur because species coexistence is promoted by environmental variability. Thus, this competing prediction is conditional on species coexistence being fluctuation-dependent.

Fluctuation-depedent coexistence comes in two flavors: the storage effect and relative nonlinearity.

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2. Advancing Theory to Link Coexistence and Ecosystem Stability. New theory . . . . storage effect only . . . . annual plant specific

3. Testing New Theory with Empirically-Based Models. Winter annual plant communities in the Sonoran Desert offer an ideal model system for testing predictions from our theoretical model.

4. Broader Significance. The broader impacts of this proposal focus on training. First, the grant will support the postdoctoral training of an early career scientist, Andrew Tredennick (the Co-PI). Co-PI Tredennick will develop a short course for graduate students at the University of Arizona on data-model assimilation. We will use the data and models from our proposed research as examples in the course material. The course material will be hosted on GITHUB so that students and faculty at other institutions can implement a similar short course. The short course therefore serves two goals: (1) Co-PI and postdoc Tredennick will gain experience devel-
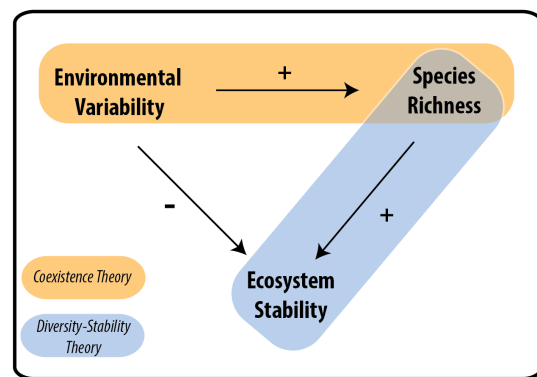

Figure 1: *An integrated theory to understand the net effect of environmental variability on ecosystem stability. Coexistence theory (in orange bubble) has focused on how environmental variability can maintain diversity by stabilizing species coexistence, while diversity-stability theory (in blue bubble) has focused on the effect of species richness on ecosystem stability. In combination, environmental variability will decrease ecosystem stability, but it may also increase species richness, which can then increase ecosystem stability. We propose new theory and empirical tests to understand the full effect of environmental variability when it also promotes diversity.*

Figure 2: Simulation results from an annual plant model with two species coexisting by the storage effect. Left panels show time series from three simulations: A) environmental variability is too low to allow coexistence; B) environmental variability is high enough to allow coexistence, but only one species is present; and C) environmental variability is high enough to allow coexistence of both species. The barplot on the right shows the coefficient of variation of total community abundance for each simulation. CV increases as environmental varition does, but fluctuation-dependent coexistence allows for portfolio effects (compare red and blue bars).
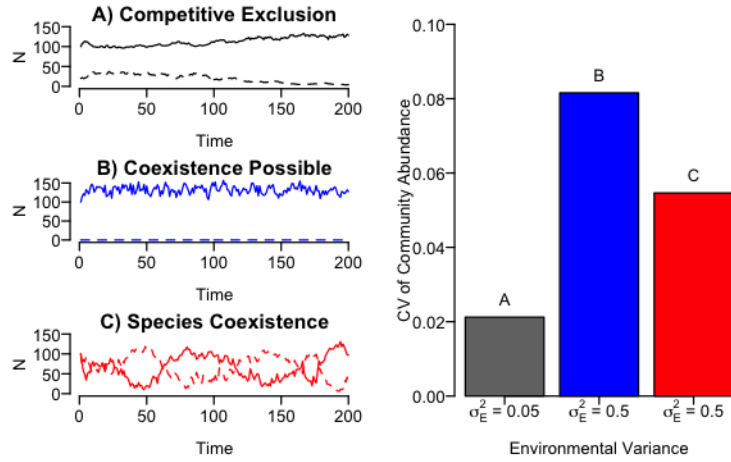
oping and teaching graduate-level courses and (2)
the wider ecological community will have a new
resource for graduate training in contemporary approachs to confronting models with data.