

## Intellectual Merit

The relationship between community diversity (number of species) and the temporal stability (variation through time) of community biomass or abundance has been debated by ecologists for over 50 years. In general, biodiversity appears to stabilize community biomass, but clear mechanisms remain elusive and our ability to predict stability in natural communities is limited. Two key questions remain: (1) What are the demographic and population processes that increase, or decrease, temporal stability? (2) What, if any, link is there between temporal stability and the mechanism(s) by which species coexist?

To answer the first question, I will use statistical and population models to extract demographic parameters from five long term plant community datasets. These parameters will allow me to quantify the contribution of environmental variation, demographic variation, and species dominance to temporal stability across diverse ecosystems. In so doing, I will conduct a robust test of new theory that predicts temporal stability and, for the first time, show how population dynamics and species interactions produce emergent stability in natural communities.

To answer the second question, I will use mechanistic, consumer-resource models to develop new theory that bridges the gap between coexistence mechanisms and temporal stability of community biomass. I will use models of fluctuation-dependent and -independent species coexistence to discover under what conditions we should expect temporal stability to be affected by interactions among coexistence mechanisms and environmental and demographic variability. New theoretical insights will be tested with empirically-parameterized population models. This work will represent a major step forward by unifying two of ecology's most dominant research agendas.

## Broader Impacts

Biodiversity is being lost at rates similar to those during Earth's major extinctions. Thus, ecologists have a societal obligation to discover the impacts of biodiversity loss. Explicitly defining how, why, and when biodiversity matters is a key step toward implementing and achieving conservation goals. Results from this work will be published in leading ecology journals and all computer code produced during this project will be made publicly available on GitHub, an online repository hosting service that allows for collaborative coding (all data for this project is already publicly available). Thus, all results will be completely reproducible and the availability of computer code related to this project will be a great resource for scientists and students learning how to implement models or advanced statistical techniques. In addition, I will produce a series of "Whiteboard Ecology" videos that introduce a theory in ecology (e.g., Tilman's  $R^*$  theory) and the mathematical representation of the theory. The videos will be linked to R code that implements the mathematical model from each video – an often missing component of instructional videos. These videos will be one of the few resources for ecologists that spans conceptual understanding to mathematical implementation and will facilitate 'learning by doing'. These activities of OpenScience through code sharing will speed up the process of science. Finally, the scientific and educational training I receive during this fellowship will prepare me to make important contributions to ecology and to graduate and undergraduate education.

## Intersection of Biology and Math

This project requires extensive mathematical and statistical modeling. I will use Integral Projection Models to extract demographic parameters necessary to confront new theory with data. Likewise, bridging the gap between diversity-stability theory and coexistence theory will involve deriving analytical solutions of equation sets and simulating plant communities. Dr. Peter Adler (Dept. of Wildland Ecosystems, Utah State University) will be my biology mentor. Dr. Fred Adler (no relation to Peter; Dept. of Mathematics, University of Utah) will be my mathematics mentor.

# Diversity-stability relationships and coexistence: new theory and empirical tests

## 1 Introduction

For over 50 years, ecologists have debated the influence of biodiversity on population, community, and ecosystem stability (temporal invariability) (MacArthur, 1955; May, 1973). There now appears to be a general consensus that diversity stabilizes community and ecosystem level biomass or abundance through time while simultaneously destabilizing individual species biomass or abundances (Tilman, 1996; Cottingham *et al.*, 2001; Loreau & de Mazancourt, 2013). However, empirical work over the last ten years has mainly focused on detecting diversity–temporal stability relationships, and our understanding of the mechanisms driving observed diversity-stability relationships remains limited. What are the demographic and population processes that increase, or decrease, temporal stability? What, if any, link is there between temporal stability and the mechanism(s) by which species coexist?

Answering these questions requires strong theory, adequate data to confront theoretical expectations, and a modeling framework under which to develop and test new ideas relating coexistence mechanisms and temporal stability. Fortunately, each of these prerequisites are now available. Recent theoretical work by de Mazancourt *et al.* (2013) provides an explicit prediction of temporal stability; longterm demographic datasets from five ecosystems (§3.2) offer unique opportunities to estimate highly-resolved demographic parameters and environmental responses (Dalglish *et al.*, 2010); and integral projection models (IPMs) show promise in disentangling coexistence mechanisms (Adler *et al.*, 2010). I propose to use these tools to achieve two goals: (1) to analyze the importance of environmental, demographic, and species’ dominance controls on temporal stability across diverse ecosystems, and (2) to develop new tests linking contemporary coexistence theory (Chesson, 2000) and diversity–stability theory (Loreau & de Mazancourt, 2013). Achieving these goals will lead to new insights about how plant population responses to environmental change will affect ecosystem stability. In an era of rapid environmental change, such fundamental knowledge is critical.

## 2 Background

MacArthur (1955), Elton (1958), and even Darwin (Turnbull *et al.*, 2012) recognized that species can compensate for each other and stabilize function in ecosystems subject to temporal environmental fluctuations. This idea underlies the ‘insurance hypothesis’ (Yachi & Loreau, 1999) which suggests stability increases with diversity because species respond differentially to environmental conditions – species A has highest growth rates under conditions X whereas species B has highest growth rates under conditions Y. Species richness confers temporal stability by broadening the range of conditions under which the community maintains function (e.g., productivity). These ‘complementarity effects’ operate in concert with ‘selection effects’ driven by dominant species.

Recently, a major theoretical advance that predicts community stability through time (de Mazancourt *et al.*, 2013) calls for a critical re-evaluation of how hypothesized mechanisms interact. The approach of de Mazancourt *et al.* (2013) expresses community temporal stability ( $CV_T$ ) as an additive function of environmental variability, demographic variability, and species dominance (selection effects),

$$(CV_T)^2 = \left( \frac{\sigma_T}{\mu_T} \right)^2 \approx \underbrace{\varphi_e \Sigma_e^2}_{\text{environmental}} + \underbrace{\Sigma_d^2 / \bar{N}_T}_{\text{demographic}} + \underbrace{\lambda}_{\text{dominance}}. \quad (1)$$

In Eq. 1,  $\varphi_e$  is the estimate of species synchrony to environmental conditions,  $\Sigma_e^2$  is mean scaled environmental variance,  $\Sigma_d^2$  is mean scaled demographic variance,  $\bar{N}_T$  is mean community cover,

and  $\lambda$  is Simpson’s concentration index (a combined measure of species richness and evenness in the community). The formulation of Eq. 1 makes it possible to quantify the contributions of species’ environmental responses, species’ demographic variation, and dominance of any particular species to stability. This new theory was designed for use with data from biodiversity-ecosystem function experiments, and therefore initial tests of the model required many assumptions to relate experimental results to the model parameters. The data I plan to use will allow more direct tests of the biological processes represented in the model. Whether the theory in Eq. 1 is robust in natural systems remains unknown; if it does hold true, we can estimate an important ecosystem service (stability) based on the responses of individual species to global changes.

While theory has advanced rapidly to help explain diversity–stability relationships, a gulf remains between work on diversity–stability relationships and work on species coexistence (but see Turnbull *et al.*, 2012). Recent work suggests there may be no quantitative link between coexistence theory on the one hand and biodiversity-ecosystem function theory on the other (Turnbull *et al.*, 2012), or that such links are elusive (Carroll *et al.*, 2011). This is likely because diversity-ecosystem function theory is still largely driven by statistical measures from experiments, with diverse models used to explain the statistics, while coexistence theory was largely unified over a decade ago (Chesson, 2000). However, the theoretical advance by de Mazancourt *et al.* (2013) presents a new opportunity to link coexistence to stability by focusing on how different coexistence mechanisms affect the additive terms in Eq. 1. We can now ask more relevant questions, for example: How do fluctuation dependent vs. independent coexistence mechanisms alter the balance of environmental variance, demographic variance, and dominance? I will use a combination of theoretical and empirical modeling to develop and test new theory to unify these two research agendas.

### 3 Proposed Work

#### 3.1 Research Objectives

My overall objective is to increase our mechanistic understanding of temporal stability in natural ecological communities. I will do so by considering how population dynamics “add-up” to produce observed stability and how coexistence among species mediates those population dynamics.

1. **Analyze contributions of demographic, environmental, and dominance to temporal stability.** I will develop statistical models of demographic rates and how they vary with environmental drivers to build multi-species IPMs for each dataset. Using the IPMs I will estimate quantities necessary to apply Eq. 1 and quantify the contributions of demographic and environmental variation and species dominance to temporal stability in natural communities. This will also be the first test of deMazancourt et al.’s (2013) new theory in natural systems.
2. **Assess influence of coexistence mechanisms on temporal stability.** Using a consumer-resource model as a starting point, I will conduct theoretical work to determine how fluctuation-dependent vs. -independent coexistence mediates temporal stability in the context of demographic and environmental variance. I will use the IPMs built under objective 1 to empirically test the new theoretical insights.

#### 3.2 Data

I will use chart quadrat datasets compiled and digitized by Peter Adler and colleagues. These datasets are composed of annual maps of all perennial plants in 1-m<sup>2</sup> quadrats over several decades in the mid-20th century (Fig. 1). The data come from semiarid plant ecosystems representing five major North American ecoregions: southern mixed prairie in western Kansas (Adler *et al.*, 2007), sagebrush steppe in eastern Idaho (Zachmann *et al.*, 2010), northern mixed prairie in eastern Montana (Anderson *et al.*, 2011), Sonoran desert grassland in southern Arizona (Anderson *et al.*,

2012), and Chihuahuan desert grasslands from southern New Mexico (Anderson *et al.* in prep.). Large inter-annual precipitation variation (daily climate data is available) in these water-limited systems provides a unique opportunity to analyze how environmental variation couples with intrinsic demographic variation to produce emergent community stability.

### 3.3 Research Methods

#### 3.3.1 Analyze contributions of demographic, environmental, and dominance to temporal stability

For the purposes of this project I will follow the general concept outlined in Eq. 1 to predict stability, but I will use more direct statistical methods to estimate the important parameters. I will also use percent cover to measure stability, which is highly correlated with biomass in these perennial plant communities and will not affect the implementation of Eq. 1. The three additive terms in Eq. 1 can be further decomposed, but I will not detail the mathematical decomposition of those terms here. Instead, I will focus on the quantities that comprise the terms in Eq. 1, of which there are five: (1) species intrinsic per capita growth rate ( $r_i$ ;  $i$  = species), (2) species' environmental variance ( $\sigma_{e,i}$ ), (3) species' demographic variance ( $\sigma_{d,i}$ ), (4) species' normalized environmental response ( $\mu_{e,i}$ ), and (5) average species' proportional cover ( $p_i$ ).  $p_i$  is easily calculated from the data. For all other parameters I will use the approach of Adler *et al.* (2010; 2012) to first fit statistical models of vital rates and then use those models to build multi-species IPMs.

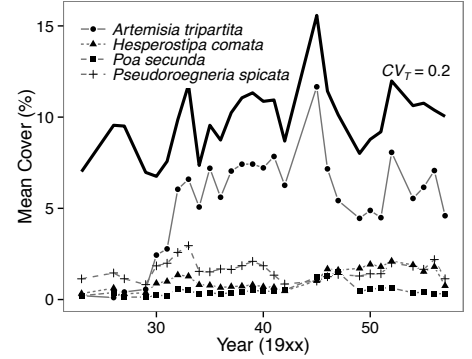


Figure 1: Time-series of dominant species' average cover from the Idaho dataset. Thick black line is average community cover with  $CV_T = 0.2$ .

Why refit statistical models of vital rates for these data when several publications (e.g. Adler *et al.*, 2010, 2012; Dalglish *et al.*, 2010) have already done so? To estimate demographic variance ( $\sigma_d$ ) requires knowledge of individual-level variation in vital rates within a species, but for statistical convenience past work using these data did not include individual random effects. So I will extend the statistical approach within a Bayesian framework to model individual-level variation. For example, a typical regression to model growth for plant  $i$  of species  $j$  in quadrat  $k$  from size  $v$  at time  $t$  to  $t+1$  ( $v_{ijk,t+1}$ ) takes the form

$$v_{ijk,t+1} = \eta_{ij,t} + \phi_{jg} + \beta_{ij,t}v_{ij,t} + \omega_j \mathbf{w}_{ij,t} + \gamma \mathbf{C}_t + \mathbf{\Gamma} \mathbf{C}_t v_{ij,t} + \epsilon_{ij,t} \quad (2)$$

with variance modeled as a nonlinear function of predicted plant size,  $Var(\epsilon_{ij,t}) = ae^{bv_{ij,t+1}}$ . In Eq. 2,  $\eta$  is a time-varying random year effect on the intercept that will vary by individual, species;  $\phi$  is the quadrat group effect;  $\beta$  is a time, individual, and species varying size effect;  $\omega$  is a vector of competitive or facilitative effects of crowding,  $\mathbf{w}$ , by each species on species  $j$ ;  $\gamma$  is a vector of climate effects corresponding to climate covariates,  $\mathbf{C}$ , on the intercept; and  $\mathbf{\Gamma}$  are the interaction effects between climate covariates and size. Using hierarchical Bayes it is straightforward to include species- and individual-level effects (Tredennick *et al.*, 2013). Regressions for other vital rates, e.g. survival and recruitment, follow similar forms.

The crux in estimating total demographic variance will be combining the different vital rate variances into a single term,  $\sigma_d$ , for Eq. 1. To determine the best way to combine vital rate variances I will build IPMs based on those models and perform elasticity tests (Dahlgren & Ehrlén, 2009) where each vital rate is perturbed to see the effect of small changes on community dynamics. Using these elasticity tests, variances will be weighted appropriately and combined. This alone will answer an

ecologically-interesting question: Does the relative contribution of variation in recruitment, growth, and survival to temporal stability change across ecosystems and species?

To estimate  $\mu_e$  and  $\sigma_e$  I will use the parameterized IPMs to model low density growth rates in the absence of interspecific interactions, isolating variation due to environmental drivers alone. This simulation will create a time series of species environmental responses ( $\mu_{e,t}$ ) for each species, the standard deviation of which will be the species-specific environmental variance  $\sigma_e$ . Armed with these parameters, I will be able to “predict” stability at each site in the dataset using Eq. 1. Critically, temporal stability of species and community cover can be directly calculated from the data (Fig. 1). For each dataset I will ensure predicted stability adequately captures observed stability before drawing further inference from the environmental and demographic components.

### 3.3.2 Assess influence of coexistence mechanisms on temporal stability

We still lack coherent, mechanistic theory that bridges the gap between diversity-stability relationships and species coexistence, but there are some hints in the literature. For example, recent work shows competition among species decreases temporal stability of community biomass by increasing the amplitude of species’ fluctuations, even as the fluctuations become more asynchronous (Loreau & de Mazancourt, 2013). In the context of fluctuation-independent coexistence, this suggests we should expect stability to depend on the strength of resource partitioning. All else being equal, stability should be higher in communities where species partition resources to minimize competition relative to communities where resource requirements overlap and competition is greater. Yet, this simple theoretical hypothesis (among others) remains untested. To do so requires moving beyond phenomenological Lotka-Volterra models that have dominated the stability literature to mechanistic models of species interactions.

As a starting point, I will use a modified MacArthur consumer-resource model for  $q$  abiotic resources ( $R$ ) and  $n$  plant consumers ( $X$ ):

$$\underbrace{\frac{dR_i}{dt} = s_i - d_i R_i - \sum_{j=1}^n c_{ji} R_i X_j}_{i=1\dots q} \quad , \quad \underbrace{\frac{dX_i}{dt} = X_i b_i \left( \sum_{j=1}^q c_{ij} w_{ij} R_j - m_i \right)}_{i=1\dots n} \quad (3)$$

where  $s_i$  is resource supply rate,  $d_i$  is the per unit resource loss rate, the matrix  $\mathbf{c}$  is the per capita uptake rate for each consumer of each resource,  $b_i$  is the conversion rate of new assimilated biomass,  $m_i$  is metabolism- and death-related biomass loss, and  $\mathbf{w}$  is a matrix of species-specific conversion factors for each resource. Differences among consumer uptake rates in  $\mathbf{c}$  can achieve coexistence by resource partitioning (fluctuation-independent).

Initial simulations of a two species-two resource community show that, counterintuitively, the strength of resource partitioning alone does not interact with environmental variance (interannual variability in  $s$ ) in terms of temporal stability of community biomass – fitness inequalities and asymmetric resource variability were also required (Fig. 2). Clearly, our understanding of stability in terms of species coexistence needs refinement. Provoked by these surprising results, I will work

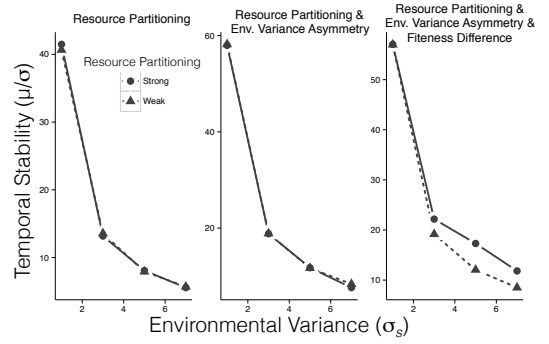


Figure 2: Effect of resource partitioning and environmental variance (temporal variance of  $s$ ,  $\sigma_s$ ) on community biomass temporal stability under different model scenarios. Asymmetric variation in  $s$  among resources and fitness differences (in  $\mathbf{w}$ ) were required to induce an interaction between resource partitioning and environmental variance. ( $x$ -axis shows  $\sigma_s$  for resource 1).

with Fred Adler to incorporate demographic variance via individual growth and to analyze models of fluctuation-dependent coexistence. I will endeavor to discover under what conditions we should expect to see interactions among coexistence mechanisms and variability, and how those conditions change with species richness. For example, it is easy to hypothesize a strong interaction between environmental variance and coexistence via relative nonlinearity or the storage effect (Chesson, 2000), but this theoretical work will explicitly delineate the parameter space under which that hypothesis holds (or not). I will test new theoretical insights using the empirically-parameterized IPMs applied to datasets with known coexistence mechanisms (Adler *et al.*, 2006, 2010).

## 4 Significance

**Intellectual Merit.** Biodiversity is being lost at rates similar to those during Earth’s major extinctions (Barnosky *et al.*, 2011). A central goal of ecology is to understand the impacts of biodiversity loss on ecosystem functioning, and to discover the mechanisms behind diversity–stability relationships in a range of natural ecosystems. This project will increase our understanding of the processes that link biodiversity and ecosystem function – an understanding that is critical to fundamental scientific knowledge and to arguments underlying conservation efforts. In an era of rapid environmental change, it is important to understand when species’ variation in responses to environmental factors primarily drives temporal stability and when demographic variation is more important. Also, two related yet distinct research agendas have dominated community ecology over the past decade: one focused on species coexistence and one on the relationship between biodiversity and ecosystem function. While it is clear these two research programs and their underlying concepts are related, few attempts have been made to formally link the two bodies of theory. The second goal of my proposed research (§3.3.2) will provide this much needed unification.

**Broader Impacts.** Strong quantitative and modeling skills are required to tackle many of the most important problems in ecology and evolutionary biology (Barraquand *et al.*, 2013). The broader impacts of this proposal focus on the distribution of modeling tools and educational videos aimed at reducing the learning curve associated with ecological theory and its formal implementation. First, all R code associated with the project (statistical models, IPMs, and theoretical simulations) will be made freely available on GitHub (<http://github.com/atredennick>), an online repository that allows for collaborative coding (the raw data for this project is already publicly available). Second, I will produce a series of ‘Whiteboard Ecology’ videos that introduce a theory in ecology (e.g.,  $R^*$ ) and the mathematical representation of the theory. The videos will be linked to R code that implements the mathematical model from each video – an often missing component of instructional videos. These videos will be one of the few resources for ecologists that spans conceptual understanding to mathematical implementation and will facilitate ‘learning by doing’. These activities of OpenScience through code sharing will speed up the process of science. Lastly, I will develop and release an R package titled `ecoTheory` that will include functions to simulate the models from the video series.

## 5 Training Objectives and Career Development

**Intersections of Math and Biology.** Answering the most difficult questions of modern ecology requires the ability to rigorously link theory and data. Throughout the course of this fellowship I will hone my data-model assimilation skills and develop a new set of analytical skills related to mathematical modeling. With Peter Adler I will learn how to implement IPMs based on cutting-edge hierarchical statistical models. With Fred Adler I will develop new expertise in theoretical ecology and analytical approaches. This will give me the toolkit to make important contributions to fundamental and applied ecology.

**Graduate and Undergraduate Education.** Mentoring mathematically literate ecologists will be a central focus of my career as a tenure-track professor at a major research institution. Thus, I want

to gain the skills necessary to teach the next generation of ecologists how to use advanced theory, cutting-edge statistics, and data to draw inference from ecological systems. My proposed sponsors have a history of producing such students. We will develop Teaching and Mentoring Statements over the course of this fellowship for faculty applications. As part of my Teaching Plan I will develop a syllabus for a new undergraduate course teaching core ecology via computer programming in R.

**Career Development.** This proposed work will extend the statistical and modeling skills I acquired during my PhD work and give me a new set of skills related to mathematical analysis. The fellowship will also represent a shift in my focus from a particular ecosystem (savannas) to more general questions of ecology, making me a more well-rounded scientist. At the start of this fellowship Peter Adler, Fred Adler, and I will have two in-person meetings at the University of Utah to discuss my ultimate career goals. In these meetings we will formalize my training plan, but we will focus on three things: (1) publication record, (2) proposal writing, and (3) teaching/mentoring. P. Adler and F. Adler both have experience on hiring committees at large universities. They will help me craft a compelling Research Statement and a complete faculty application package.

## 6 Justification of Sponsoring Scientists and Host Institution

Peter Adler, my proposed Biology mentor and lead sponsor, has made several substantial contributions to ecology by combining theory, process models, and data (e.g., Adler *et al.*, 2010). He has also curated the long-term datasets I plan to use in this study. Dr. Adler will be an excellent mentor because of his experience parameterizing models with long-term data to test a theoretical question. Likewise, his detailed knowledge of species coexistence mechanisms will help me integrate coexistence and stability theories (Turnbull *et al.*, 2012). I will interact with postdocs, graduate, and undergraduate students in Dr. Adler’s lab, and will also have opportunities to work with his wide network of colleagues (see Adler *et al.*, 2011). In addition to Dr. Adler’s lab, USU is home to the Ecology Center, a cross-college hub that hosts a diverse array of ecologists. USU’s *Center for Innovative Design and Instruction* (<http://cidi.usu.edu/>) will aid in achieving the broader impact goals of this project.

Fred Adler (no relation to Peter Adler), my proposed Mathematics mentor, is a widely known bio-mathematician who has successfully brought basic mathematics to bear on applied biological problems. His home institution, the University of Utah, where he has dual appointments in the Mathematics and Biology Departments, is only 1.5 hours from USU which will facilitate collaboration. He is also the director of the Center for Quantitative Biology, which will provide me opportunities to collaborate with and learn from a variety of quantitative life scientists. Dr. Adler will be an excellent mentor because of his experience training mathematical ecologists. In fact, he was recently recognized with the University of Utah’s Distinguished Mentor award.

## 7 Timetable of Yearly Goals

Year	Research/Training Goals	Broader Impacts	Teaching/Mentoring
1	Fit statistical models; build IPMs; learn to derive analytical solutions; submit first publications	Produce 3 “Whiteboard Ecology” videos; create accessible repo on GitHub	Take role in mentoring undergrads; develop Mentoring Philosophy with both mentors
2	Stability analyses; submit publications; chair session at annual meeting; Research Statement	Produce 4 “Whiteboard Ecology” videos; develop ecoTheory package	Consult with CIDI* on syllabus; Teaching Statement
3	Use IPMs to test theoretical predictions on stability-coexistence; submit final publications	Release ecoTheory package on CRAN	Run parallel lab for USU ecology course in R; create teaching portfolio

\*USU’s *Center for Innovative Design and Instruction* (<http://cidi.usu.edu/>)

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## Data Management Plan

1. **Data.** The annually mapped chart quadrat data for this proposed project are already publicly available on the web as *Ecological Archives* (see citations below) or will be soon (e.g., Chihuahuan desert grassland data; Anderson *et al.* in prep). No new data collection is planned as part of this project.
2. **Computer Code.** All computer code (primarily R code) produced during the project will be made publicly available on GitHub (<http://github.com/atredennick>). As results are published, computer code for specific publications will be published as supplementary documents and archived on GitHub. Thus, all results will be completely reproducible.
3. **Personnel Responsibilities.** Andrew Tredennick will be solely responsible for the archiving and management of computer code after the project ends. Peter Adler will remain in sole charge of the chart quadrat datasets he has curated.

*Link to all data:* <http://www.cnr.usu.edu/htm/facstaff/adler-web/adler-datasets>

## Data Citations

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## Teaching Plan

*“Studying biological dynamics requires a greater emphasis on modeling, computation, and data analysis tools than ever before.”*

-AAAS, Vision and Change in Undergraduate Education: A Call to Action

### 1 Introduction

Regardless of discipline, the scientific, cultural, and technological advances of 21st Century will be made by those who write computer code. Building on the broader impacts associated with my Research Plan, my Teaching Plan will focus on efforts to bring programming skills into undergraduate ecology education. While this plan does include hands-on teaching experience, much of it is directed toward my own development as an educator and toward developing novel curricula to successfully combine teaching of programming skills coincident with core concepts of biology and ecology.

### 2 Why Computer Modeling for Undergraduates?

The AAAS report *Vision and Change* (Brewer & Smith, 2011) clearly states the importance of modeling and simulation in the biological sciences. Indeed, the “ability to use modeling and simulation” in the context of complex systems is one of six desired “core competencies” for undergraduate biology majors (and is related to many of the other five core competencies). These same activities can also lead to better learning outcomes more generally. For example, the abstract nature of computer coding relative to ‘table-based’ simulations in Excel requires students to make an important cognitive leap to abstract thinking.

Active computer programming may be the best way to achieve several learning objective simultaneously, regardless of a student’s preferred learning style. Kolb (1981) defined four “learning types”: accomodators, divergers, convergers, and assimilators. In brief, accomodators enjoy hands-on, active learning with concrete examples; divergers prefer reflective observation and discussions; convergers like to work with “things” and excel at abstract conceptualization; and assimilators like to compile large amounts of data to construct theories. In any given classroom there will be a variation of learning types among *and within* students.

How do we as educators cope with such variability? For the case of ecology, I propose one way to overcome the multitude of learning types is through computer modeling. Kolb (as cited in Nilson, 2003) prescribed teaching recommendations for each of the learning types. For all but assimilators, simulation was a suggested technique. While simulation means different things in different disciplines, in ecology computer simulation of dynamic processes is an obvious technique, and one that is increasingly recognized as imperative to the biological sciences (Brewer & Smith, 2011). Furthermore, computer programming skills, along with attendant critical thinking and problem solving skills, are highly desirable on the job market regardless of discipline (Casserly, 2012). Not only will undergraduates better grasp biological principles, they will have a measurable skill that will increase their employment prospects. I will perform a formal assessment to test whether computer coding offers benefits beyond Excel-based simulations (§4.2).

### 3 Training Objectives

The main goal of this Teaching Plan is for me to gain the skills necessary to become an effective educator at the outset of my faculty career. To do so requires increasing my knowledge of contemporary pedagogical theory and successfully integrating that theory into teaching, syllabus development, and mentoring. This plan is centered on three objectives. Importantly, specific activities under each objective will involve formal assessment (described in §4).

1. **Syllabus development.** I will develop a syllabus for a new undergraduate ecology course centered on computer simulations. The syllabus will be “learning-centered” and incorporate ideas from objective 3.
2. **Teaching and mentoring experience.** I will gain hands-on teaching experience, as well as test the waters of teaching computer simulation to undergraduates, by leading several laboratory exercises in an existing ecology course at Utah State University. I will also take a role in mentoring undergraduate students in Peter Adler’s lab.
3. **Core education training.** I will read and discuss contemporary pedagogical literature and theory with Peter Adler. I will attend teaching workshops and discussion groups held at Utah State University and the University of Utah.

## 4 Training Methods

### 4.1 “Learning-Centered” Syllabus

The course I plan to develop is centered on computer programming of ecological models but also has higher-level objectives. These include critical thinking and problem-solving skills. To ensure both higher-level and lower-level (e.g., mastery of ecological concepts) objectives are met, I will construct a syllabus based on learning objectives. Following Nilson (2003), the learning objectives I develop will contain three parts: (1) statement of measurable performance, (2) statement of conditions for the performance, and (3) criteria and standards for assessing the performance. I will start by explicitly defining the ultimate learning objectives of the course, and then work backwards to build the course toward the eventual goal. I will choose content most suited to helping students achieve the outlined learning objectives.

After developing the learning objectives and deciding on course content, I will write a “complete syllabus” (*sensu* Nilson, 2003) that includes a proposed schedule and weekly readings, assignments, and laboratory exercises (see below for example). Utah State University’s *Center for Innovative Design and Instruction* (CIDI, <http://cidi.usu.edu/>) offers consultation services for syllabus design, so I will work closely with CIDI while writing my syllabus. The class will be a “flipped course” where lectures introducing concepts and models are posted online and all homework and modeling exercises are done in class with full participation from the instructor. Flipped courses are student- and learning-centered, allowing students to gain deeper understanding of the material, to be active participants in the class, and to receive real-time feedback (Bergmann & Sams, 2012). This feedback also benefits the instructor by offering endless opportunities to adjust teaching styles and materials. Various faculty at USU and CIDI consultants will provide critical feedback on the syllabus.

A key component of the syllabus will be lab sessions centered around computer programming of biological models. Since the class will be oriented toward undergraduate students, it will be important to foster mathematical and programming confidence and intuition. To do so, introductory labs will focus on established models, but in unique (and fun) contexts. For example, one lab could use simple models of disease transmission (*Susceptible, Infected, Recovered* (*SIR*) models)

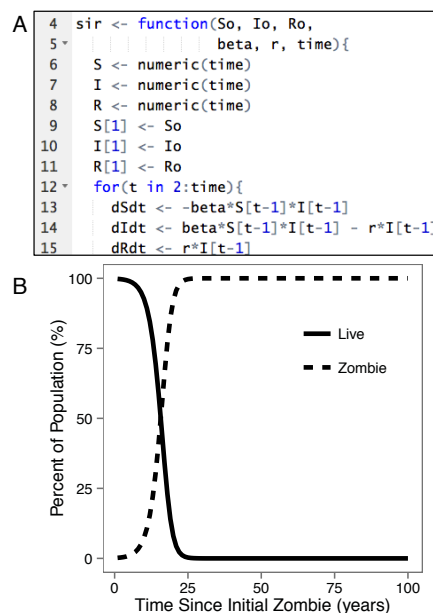


Figure 1: Simulating the zombie apocalypse. (A) The model is very simple (two parameters) and the core function only takes about 10 lines of code. (B) The model output showing 100% infection (zombie state) over time.

to simulate a zombie apocalypse and show how the end results will always (eventually) be 100% infection (Fig. 1). This will get students to start thinking about how equations are put together via non-intimidating examples. After mastering the “easy” topics, the same models can be extended to simulate more “real” topics such as the transmission and recovery of chronic wasting disease in deer populations (Miller *et al.*, 2006). Using non-ecological, fun simulation problems will give students mathematical intuition and programming confidence to tackle more complex ecological problems.

## 4.2 Teaching Experience

No amount of planning can prepare one for the rigors and uncertainties of actually teaching. To complement my extensive non-teaching education training, I will teach several parallel lab sessions for an established undergraduate population ecology class at Utah State University taught by Dr. David Koons. Dr. Koons’ class already involves quantitative modeling and simulation, but is currently taught exclusively using Microsoft Excel. As a pilot lab for my proposed course in §4.1 I will offer an advanced section of Dr. Koons’ lab taught in R. For example, one of the first lab exercises is to model density-independent growth via an exponential equation. This is easy to implement in R and will give students confidence before moving to later topics like matrix models. With Dr. Koons, I will choose five lab sessions to offer in parallel. Students choosing the R option will conduct all other labs in Excel – this will allow an opportunity for formal assessment (see below).

Peter Adler and David Koons will provide formal feedback on my teaching. Likewise, students will be asked to give feedback in real time following each laboratory section. These comments will be anonymous and guided by prompts. To formally assess if computer simulation in R (which requires coding) is more effective than simulation using Excel (no coding required) I will compare student performance on exam questions. I will design statistical tests that control for student differences and self-selection into the advanced lab group.

## 4.3 Education Training and Mentorship

During the 3rd year of this fellowship, I will attend a one week “Faculty Bootcamp” hosted by The University of Utah’s Center for Teaching and Learning Excellence (CTLE, <http://ctle.utah.edu/>). I will also attend the semi-monthly “Teaching Workshop Series” also hosted by CTLE at the UofU. The workshops cover a range of topics from hybrid course design to teaching students with disabilities. I will also sit-in on classes taught by Peter Adler at USU and Fred Adler at UofU. Peter Adler teaches an undergraduate “Wildland Ecosystems” course (similar to a course I have co-instructed at Colorado State University) and Fred Adler teaches an undergraduate “Modeling Biological Dynamics” course.

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