Do species-environment feedbacks lead to multiple trajectories of ecosystem change?
KEY WORDS: *dynamic feedback, ecosystem services, species-environment interactions*

INTRODUCTION: This proposal seeks to understand how species-environment interactions and feedbacks among those interactions alter ecosystem function through time. When an ecosystem is perturbed, is functional properties are likely to change [1-2]. However, it is still a mystery how these changes play out over time. In some cases, ecosystems eventually return to their pre-disturbed state. In others, they appear to be drawn towards a number of alternative states as complex feedbacks among species and their environment "pull" ecosystems along diverging trajectories. Since the functional properties of ecosystems change along different parts of these trajectories and states [1], an open question is whether these feedbacks can be used to change ecosystem trajectories and foster desirable ecosystem services.

I would investigate this question by building on a unique dataset spanning 30 years of grassland studies and experiments conducted at the Cedar Creek Ecosystem Science Reserve, MN (CDR). Rather than focusing on the immediate results of species and environmental manipulations as many studies have in the past [3-6], I propose to analyze the dynamic trajectories that ecosystems follow as they recover from such manipulations. I will do this by comparing observed trends at CDR to theoretical expectations of how species and environments should alter one another through time. This research would provide a mechanistic explanation for ecosystem function, and the provisioning of ecosystem services at large.

I will focus on a cross-section of ecosystem functions – ***biomass production***, ***soil carbon sequestration***, and ***enhancement of ground water quality*** – that pertain to well-known ecosystem services. Within experimental plots at CDR, species and resource composition have been systematically manipulated for decades (*e.g.* selective weeding or nutrient addition) [3,6-8]. These manipulations not only significantly alter the immediate production of ecosystem services in plots, but also how those services change through time following the manipulation – that is, the trajectory of those ecosystem services [4-5, 8]. Most intriguingly, plots whose treatments were abandoned ten years ago have not reverted to their pre-manipulation states. Though they may be approaching such a state in the distant future [7], these dynamics suggest the possibility of multiple trajectories leading to different functional states among ecosystems.

Hypothesis: **The persistent changes in ecosystem service trajectories observed at CDR result from species-environment feedbacks.** Selective manipulation of these factors could therefore change the natural rate of existing system dynamics, or fundamentally alter the trajectory along which ecosystems evolve, leading them towards alternative functional states. As a result, such manipulations could lead to low-input management strategies that maintain ecosystem services though natural feedback mechanisms.

RESEARCH PLAN: The experiments at CDR document intriguing but unexplained patterns. We still lack the analysis and modeling approaches needed to take advantage of species-environment feedbacks in ecosystem management. To do so, we must: (1) identify possible ecosystem trajectories (2), determine which species-environment feedbacks are most important in moving the system along these trajectories, and (3) develop management practices that encourage feedbacks that enhance desired ecosystem services over realistic timescales.

Part I. **Meta-analysis and model of historical trends.** I first will compile data from studies at CDR, and take new measurements to document dynamics among the three focal ecosystem services. I will next build a ***transition matrix model*** detailing how these ecosystem services change over time following experimental manipulations. I will then identify species and resource manipulations that likely contribute to these ecosystem dynamics (*e.g.* specific combinations of species and resources that are significantly associated with increased soil carbon sequestration). Previous studies suggest that only a handful of resources control species abundance at CDR [3-4,6], and that there are physical limitations to types of interactions species and environments can interact (*e.g.* maximum soil fertility or water capacity) [4,6].

Part II. **Theoretical model of dynamics.** Historical experiments at CDR represent only a small snapshot of the total possible manipulations and long-term system dynamics. To expand this view, I will use physiological data from CDR and relevant theoretical literature to parameterize a ***resource competition model*** that quantitatively predicts interactions among the species and resources identified in ***Part I***. This model will both account for life history characteristics shared among plots (*e.g.* disease, climate), and species-resource dynamics specific to manipulated plots. I will then match dynamics in this theoretical model to those observed in ***Part I*** to estimate how ecosystem service trajectories are expected to change as a result of species-environment interactions, and identify regions within this model that maximize the three focal services. I will then work backwards from these "desirable" regions using dynamic programming optimization to identify trajectories, and corresponding manipulations, that that should "nudge" existing plots towards these desirable states over realistic timeframes.

Part III. **Field-testing model.** I will then design a novel series of field experiments to test this model. In these experiments, I will apply the management prescriptions identified in ***Part II*** and observe corresponding changes in plot species composition, resource abundance, and ecosystem service production. Where these dynamics would take too long to observe myself, I will measure changes in abandoned experiments and successional gradients at CDR to document the natural trajectories that ecosystems follow when manipulations have ceased. If the feedbacks identified in my model explain the trends in these experiments, I will have found convincing support for my hypothesis. Even in the absence of feedbacks and alternative states, I may be able to identify species-environment interactions that temporarily alter the provisioning of services (*i.e.* slow the rate at which natural dynamics "undo" system management).

Intellectual merit: The implications of this project are not trivial. Managers have extensive experience in using high-input, continuous management to maintain particular services against natural gradients of ecological change (*e.g.* high-yield agriculture) [9]. However, as demands for ecosystem services, such as food, water, and energy production increase while the area available per person to supply those services decreases [2], it becomes increasingly important to understand whether – and if so what – more modest and targeted interventions can "nudge" ecosystems towards desirable states. The method I propose to devise would provide a general framework for designing these sorts of strategies worldwide.

BROADER IMPACTS: **Education and collaboration at CDR.** I will use my experience in EnviroEd to mentor interns and build curriculum within the established intern and education programs at CDR. As I did in summer 2011, I will work with educators at CDR to teach this curriculum to K-12 students, teachers, and representatives from the American Chippewa tribe. Additionally, I will work with farmers from the towns around CDR to investigate ecosystem services and management regimes that the local community finds valuable. Since their farms are regionally similar to CDR, but differ significantly in their management history, collaboration with these communities would contribute immensely to the breadth of my study.

SOURCES: **[1]** Kylafis *et al.* (2011) *Ecology Letters* **14:**82-90. **[2]** Carpenter S *et al.* (2009) *PNAS* **106**:1305–1312. **[3]** Knops J *et al.* (2000) *Ecology* **81**:88-98. **[4]** Symstad A (1998) *Oikos* **81**:389-397. **[5]** Tilman D (1987) *Ecology Letters* **57**:189-214. **[6]** Wedin *et al.* (1990) *Oecologia* **84**:433-441. **[7]** Tilman D (1994) *Ecology* **75**: 2-16. **[8]** Tilman D *et al.* (2006) *Science* **314**:1598-1600. **[9]** Tilman D (1999) *PNAS* **96:**5995–6000.