A report to the LTER Network Office on "A synthesis of LTER community data to test metacommunity theory under different ecological conditions"

Supplementary funding for postdoctoral support for Eric R. Sokol (sokole@vt.edu) in collaboration with J. E. Barrett and Bryan L. Brown for FY 2013.

## **Summary**

One of the major goals of ecology is to understand how biodiversity is organized at local and regional scales, and how the main drivers of diversity vary across different ecosystem types. The metacommunity concept has proven to be a major advance toward understanding the influence of local and regional drivers of biodiversity. A metacommunity refers to a group of multi-species assemblages of organisms in an ecosystem that are linked through dispersal. Diversity patterns in a metacommunity may be influenced by both local environmental conditions (niche-based species-sorting by environmental filters) and dispersal dynamics. The aim of this project was to develop computer-based simulations of metacommunities to estimate how common measures of biodiversity respond to different types of shifts in metacommunity dynamics. We then used the modeled links between biodiversity outcomes and model parameters to assess how observed biodiversity patterns across different ecosystems in the LTER network are structured by different metacommunity dynamics.

For this project, a metacommunity simulation model was developed from previous work (Sokol et al. 2011) into an add-on package for the R statistical environment (MCSim). This software was used to simulate biodiversity outcomes under different levels of control by dispersal-based and niche-based metacommunity dynamics on the HokieOne super computer at the Advanced Research Computing facility at Virginia Tech. The simulated diversity outcomes were used to conduct a sensitivity analysis of the different types of factors that can influence perceived biodiversity patterns.

Model parameters assessed in the sensitivity analysis represented the following characteristics of a metacommunity

- The legacy influence of the initial regional species richness and evenness
- Rate of introduction of novel species into the metacommunity
- Spatial scale of environmental heterogeneity
- Spatial scale heterogeneity in the distribution of individuals
- Dispersal limitation modeled as the slope of the dispersal kernel
- Immigration rates
- Environmental filter specificity for a particular functional trait
- Functional diversity in the species pool
- Size and variation in size of local assemblages

Biodiversity was partitioned into alpha (local), beta (among site differences in composition), and gamma (regional) components, and the strength of correlation between beta-diversity and spatial and environmental variables was examined under different types of simulated metacommunity scenarios.

We found that diversity metrics calculated using presence/absence data, which are more sensitive to shifts in the rare-biosphere, are more sensitive to different model parameters than diversity metrics based on relative abundances, which are more sensitive to shifts in the dominant species. Beta-diversity, when calculated using presence/absence data, was most sensitivity to the level of functional diversity present in the regional species pool and the level of connectivity among the assemblages that made up the metacommunity. When calculated using relative abundances, beta-diversity was sensitive to (listed in

order of importance) functional diversity, metacommunity openness (probability of invasion of a novel species), among-site connectivity, assemblage size, and the number and abundances of species used to initiate the simulation.

Variation partitioning is an analysis used to estimate the degree to which biodiversity (measured as beta-diversity) is linked to environmental variation, and how much is driven by spatial patterns that occur from spatially autocorrelated dispersal dynamics. The analysis showed the environmental and spatial components were sensitive to different types of metacommunity dynamics. The relationship between beta-diversity and environmental gradients was stronger in simulations with greater functional diversity in the regional species pool. The spatial arrangement of environmental gradients influenced beta-diversity only when abundances were used to calculate biodiversity. Spatial structure in beta-diversity, independent of environmental gradients, was most sensitive to immigration rates.

We used the simulations to estimate the relationship between model parameters and biodiversity patterns to interpret differences in biodiversity patterns among different types of metacommunities across the LTER network. We included data sets representing seven aquatic and five terrestrial ecosystems from the BES, CWT, FCE, MCM, and ARC sites as well as data from the Calhoun Experimental Forest. Organisms represented in the meta-analysis include zooplankton, bacteria, fungi, macroinvertebrates, diatoms, fishes, cyanobacteria, and nematodes. We calculated alpha, beta, and gamma diversity as well as the spatial and environmental components of beta-diversity for each data set and used these diversity metrics to compare the observed data sets against the simulated data sets. By using this comparison, we inferred the relative influence of different metacommunity dynamics across the LTER sites included in this study.

Using this method to assess the importance of functional diversity, we found soil fungal communities to exhibit biodiversity patterns more strongly indicative of niche-based species sorting. Soil cyanobacterial communities in the McMurdo Dry Valleys in Antarctica was the most neutral, meaning niche-based species sorting was weakest in this data set. Simulated shifts in diversity associated with immigration rates suggested cyanobacteria and diatom communities in the McMurdo Dry Valleys in Antarctica represented metacommunities with relatively isolated local assemblages, whereas soil fungal diversity appeared to represent a highly interconnected metacommunity.

The modeling and simulation-based approach provides a method for relating shifts in biodiversity to different metacommunity dynamics. This represents a first step toward understanding the types of dynamics that can explain differences in biodiversity across the LTER network.

#### Accomplishments

In this study, we were able to make a significant advance in metacommunity theory in that we developed a conceptual metacommunity model that is general to all ecosystems, and we were able to develop this into a functioning model in the R statistical environment. Using the Advanced Research Computing resources at Virginia Tech, we were able to conduct a sensitivity analysis of this metacommunity model, which provides a universe of possible diversity outcomes given the theoretical assumptions of metacommunity dynamics. This is a significant advance in metacommunity theory and we are preparing a manuscript for peer review publication.

The LTER network provides an ideal data source for comparing observed biodiversity patterns against the numerical predictions of the metacommunity simulations. This study is the first, to our knowledge, that has created a unified metacommunity model, translated it to numerical predictions of diversity patterns, and mapped observed data sets onto the modeled parameter space. This is a powerful tool that can be used

to understand how ecology and study design interact to create the diversity patterns that are observed *in situ*.

Because of the funding made available from the LTER Network Office, we were able to travel to two conferences and conduct three meetings with collaborators in which we were able to introduce the MCSim package to peers and receive feedback. These trips provided important opportunities for us to publicize the MCSim package, written for our analysis, as a freely available software product that can serve as a tool for making predictions about how biodiversity can respond to shifts in the environment, and for analyzing the different components of biodiversity and estimating the relative influences of spatial and environmental variables. Details from these trips are described below.

Travel to the Ecological Society of America in Minneapolis, MN (August 4 - 10, 2013). The purpose of this trip was to present results from the funded project to the Ecological Society of America, to gain feedback from peers, to solicit for more data sets for the meta-analysis, and to promote the R package that is a product of this work (MCSim). The talk was titled "Linking local and regional metacommunity dynamics to diversity outcomes."

Travel to University of Maryland, Baltimore County in Columbia, MD (August 29 – 30, 2013). This trip was organized by Eric Sokol, who brought a graduate student (Brett Tornwall) and collaborator (Bryan Brown – listed as a collaborator on the proposal) from Virginia Tech to UMBC to work with Chris Swan (a co-PI at the BES LTER site) to discuss and write a manuscript relating to the BES data set that was used in the meta-analysis for the funded project.

Travel to Florida International University in Miami, FL (September 11 – 15, 2013). The purpose of this trip was to meet with co-PIs (Evelyn Gaiser, Joel Trexler), graduate students (Sylvia Lee, Mike Bush), and research technicians (Chris Catano, Jacob Bransky) associated with the FCE LTER, and give a workshop on how to analyze metacommunity data sets and run metacommunity simulations using the MCSim package for R. The MCSim (metacommunity simulation) package is currently available at <a href="http://sites.google.com/site/metacommunitysimulation/">http://sites.google.com/site/metacommunitysimulation/</a> and was written by Eric Sokol for the funded project. The tutorial developed for this workshop is available for download at the website.

Travel to Joint Genome Institute in Berkeley, CA (September 15 – 18, 2013). The purpose of this trip was to meet with collaborators (Craig Cary, Charles Lee, Craig Herbold) who helped Eric Sokol and Jeb Barrett collect and analyze soil microbial community data from the MCM LTER site. During the meeting, they discussed the analysis of the microbial community data used in the funded meta-analysis and worked on a manuscript that is a follow up to Sokol et al. (in press at Ecosphere), which is a description of metacommunity patterns for soil bacteria at the MCM LTER site.

Travel to the Transantarctic Science Meeting (TAM Science) in Minneapolis, MN (Sept 23 – 25). The purpose of this trip was to participate in the TAM (Transantarctic Mountain) Science meeting (details at <a href="www.tamcamp.org">www.tamcamp.org</a>) to present results related to the MCM LTER in a talk titled "Local and regional influences over soil microbial meta-communities in the Transantarctic Mountains", and introduce the metacommunity simulation package (MCSim). Eric Sokol was involved in the planning committee for this meeting. Some of his travel was covered by the meeting and he is only requesting funds for expenses that were not covered.

## **Products**

Peer review publications:

- Sokol, E. R., C. Herbold, C. K. Lee, S. C. Cary, and J. E. Barrett. *in press*. Local and regional influences over soil microbial metacommunities in the Transantarctic Mountains. Ecosphere.
- Sokol, E. R., J. M. Hoch, and J. C. Trexler. 2013. Metacommunity structure along resource and disturbance gradients in Everglades wetlands. Wetlands. DOI:10.1007/s13157-013-0413-1

# Conference Proceedings:

- Sokol, E. R, C. Herbold, C. K. Lee, S. C. Cary, and J. E. Barrett. 2013. Local and regional influences over soil microbial metacommunities in the Transantarctic Mountains. 1st Annual Transantarctic Science Meeting, Minneapolis, MN.
- Sokol, E. R., J. E. Barrett, B. L. Brown, and J. C. Trexler. 2013. Linking local and regional metacommunity dynamics to diversity outcomes. 98th Annual Meeting of the Ecological Society of America, Minneapolis, MN.
- Sokol, E. R., B. Tornwall, C. C. Carey, C. Swan, B. L. Brown. *submitted oral presentation, to be presented Oct* 22, 2013. Linking management to metacommunity dynamics in ponds. BES site meeting.

# Workshops:

An introduction to using MCSim, a metacommunity simulation package for the R statistical environment, to analyze biodiversity data sets. A workshop presented by E. R. Sokol September 12-13, 2013 at Florida International University for PIs and graduate students associated with the FCE LTER site.

#### Other products:

- Sokol, E. R. 2013. MCSim: a metacommunity simulation package for the R statistical environment. <a href="http://sites.google.com/site/metacommunitysimulation/">http://sites.google.com/site/metacommunitysimulation/</a>.
- Sokol, E. R. 2013. An introduction to MCSim: a MetaCommunity Simulation package for ecologists using the R statistical environment. <a href="http://sites.google.com/site/metacommunitysimulation/file-cabinet/MCSim\_tutorial.pdf">http://sites.google.com/site/metacommunitysimulation/file-cabinet/MCSim\_tutorial.pdf</a>.
- Sokol, E. R. B. L. Brown, J. E. Barrett, et al. *manuscript in prep*. A synthesis of biodiversity data to test metacommunity theory under different ecological conditions.
- Sokol, E. R., B. Tornwall, C. C. Carey, C. Swan, B. L. Brown. *manuscript in prep*. Linking management to metacommunity dynamics in ponds.

### **Participants**

Collaborators who provided information and data used in the meta-analysis include Byron Crump (ARC), Chris Swan (BES), Mike Strickland (Calhoun Exp. Forest), E. F. Benfield (CWT), Evelyn Gaiser (FCE), Sylvia Lee (FCE), Joel Trexler (FCE), Jeb Barrett (MCM), Craig Cary, Charles K. Lee, Craig C. Herbold, Diane McKnight (MCM), Tyler Kohler (MCM), Myriam de Haan (MCM), Diana Wall (MCM), and Zachary Sylvain (MCM)

Inigo San Gil (LNO) is collaborating with us to post data sets with EML metadata to the metacat database.

Chris Swan (BES), Bryan Brown (Virginia Tech), Brett Tornwall (graduate student at Virginia Tech), and Cayelan Carey (Virginia Tech) participated in a workshop to use MCSim output and data form the BES site to collaborate on a manuscript to submit for peer review.

Joel Trexler, Evelyn Gaiser, Sylvia Lee, Jacob Bransky, Chris Catano, and Mike Bush participated in a workshop at the FCE site at Florida International University on using MCSim to analyze biodiversity in large data sets, and use simulations to test ecological hypotheses about biodiversity.

Charles K. Lee (University of Waikato, New Zealand), Craig Herbold (Joint Genome Institute and Univ. of Deleware), and Craig C. Cary (University of Waikato, New Zealand) participated in a meeting to collaborate on a manuscript based on data from the MCM site to submit for peer review, and to provide feedback on microbial data for the meta-analysis.

# **Impact**

# Contributions within the discipline:

The intellectual merit of this research is the conceptual development of a unified model to describe metacommunity dynamics, the production of a mathematical representation of this model, and a software package that can be distributed to other researchers and educators. Ecologists have long tied shifts in biodiversity to various shifts in metacommunity dynamics, but this model provides a significant step toward actually linking numerical predictions to ecological hypotheses. Further, the sensitivity analysis of the model is a first step toward understanding how different metacommunity dynamics interact to create unpredictable shifts in biodiversity. Feedback from conference presentations and workshops has demonstrated a broad interest in our approach among ecologists.

A second major contribution of this project is a synthesis of LTER metacommunities, using the modeled data. The LTER data set provides a diverse array of ecological contexts over which to explore the links between ecosystem characteristics, study design, and perceived metacommunity dynamics that are manifested as different types of diversity patterns.

# Contributions to other disciplines:

Our research contributes a greater understanding of the processes that promote biodiversity. Because we have created a software product, the MCSim package, we hope to integrate a theoretical understanding of the mechanisms that drive biodiversity patterns with models used by land and resource managers and conservation biologists. Our product is open source and written in a language that can be easily implemented with other platforms (i.e., GRASS GIS and ArcGIS) to predict diversity patterns in real landscapes.

Contributions to resources for research and education:

In collaboration with Joel Trexler at Florida International University, we have created a workshop to teach PIs, graduate students, and research techs how to analyze broad scale patterns in biodiversity using large data sets. We have also worked to create exercises for graduate level ecology courses to teach graduate students how to analyze similar data sets and how to use simulations in ecology to address broad ecological questions.

# Changes/Problems

We have no changes or problems to report.