Testing the Spatial Predictions of the Maximum Entropy Theory of Ecology

Daniel McGlinn[1], Xiao Xiao[1], Justin Kitzes[2], Ethan White[1]

[1]Dept. of Biology & the Ecology Center, Utah State University [2]University of California Berkley

Introduction

Many macroecological patterns may simply reflect emergent statistical phenomena rather than specific ecological processes.

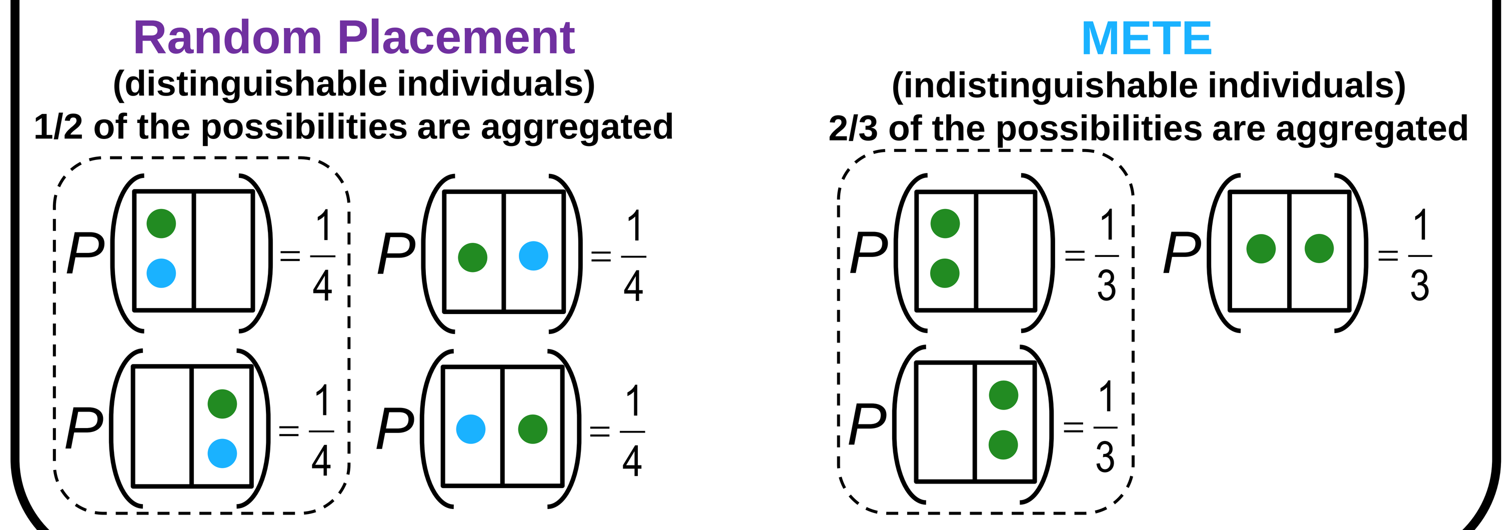
The Maximum Entropy Theory of Ecology (**METE**) takes advantage of this fact to unify community patterns through four state variables: 1) *number of species*, 2) *number of individuals*, 3) *energy,* 4) *area*.

METE ignores specific ecological processes operating below the level of the state variables. METE asserts that ecological patterns should be characterized by the most likely state of the system that maintains empirically observed constraints on the state variables.

We develop and test the spatially explicit predictions of METE using the species-area and distance-decay relationships across a diverse set of plant communities.

Two Models of Spatial Pattern

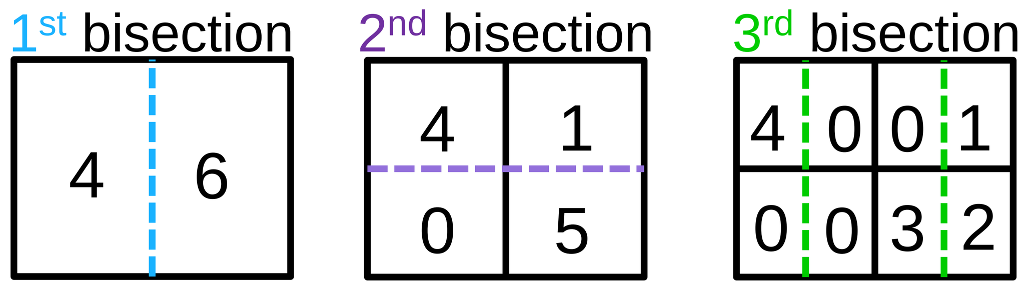
- Random placement assumes that individuals are **distinguishable**
- METE assumes that individuals are **indistinguishable**
- **Hypothesis of Equal Allocation Probability (HEAP)**
  - all unique spatial arrangements of individuals are equally likely
- Under HEAP, if two individuals are placed in either the left or right half of a quadrat, there is a higher probability that individuals will be aggregated if they are indistinguishable



Spatial Simulation Approach

We developed the spatially explicit predictions for METE by iteratively bisecting an area and applying **HEAP** until the spatial grain of interest was achieved.

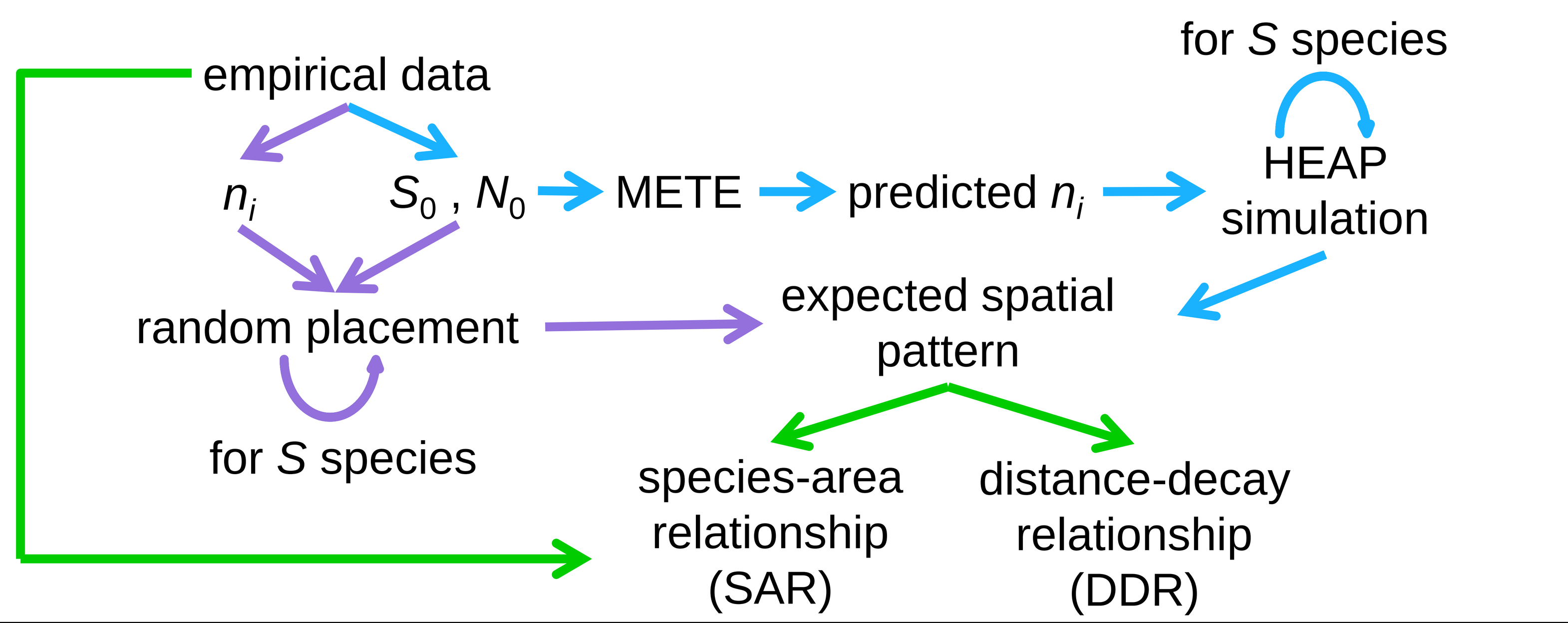
For example, with 10 individuals and 3 bisections



At each bisection the individuals are randomly placed on either side of the bisection line, this can quickly generate spatially aggregated patterns of individuals.

Objectives

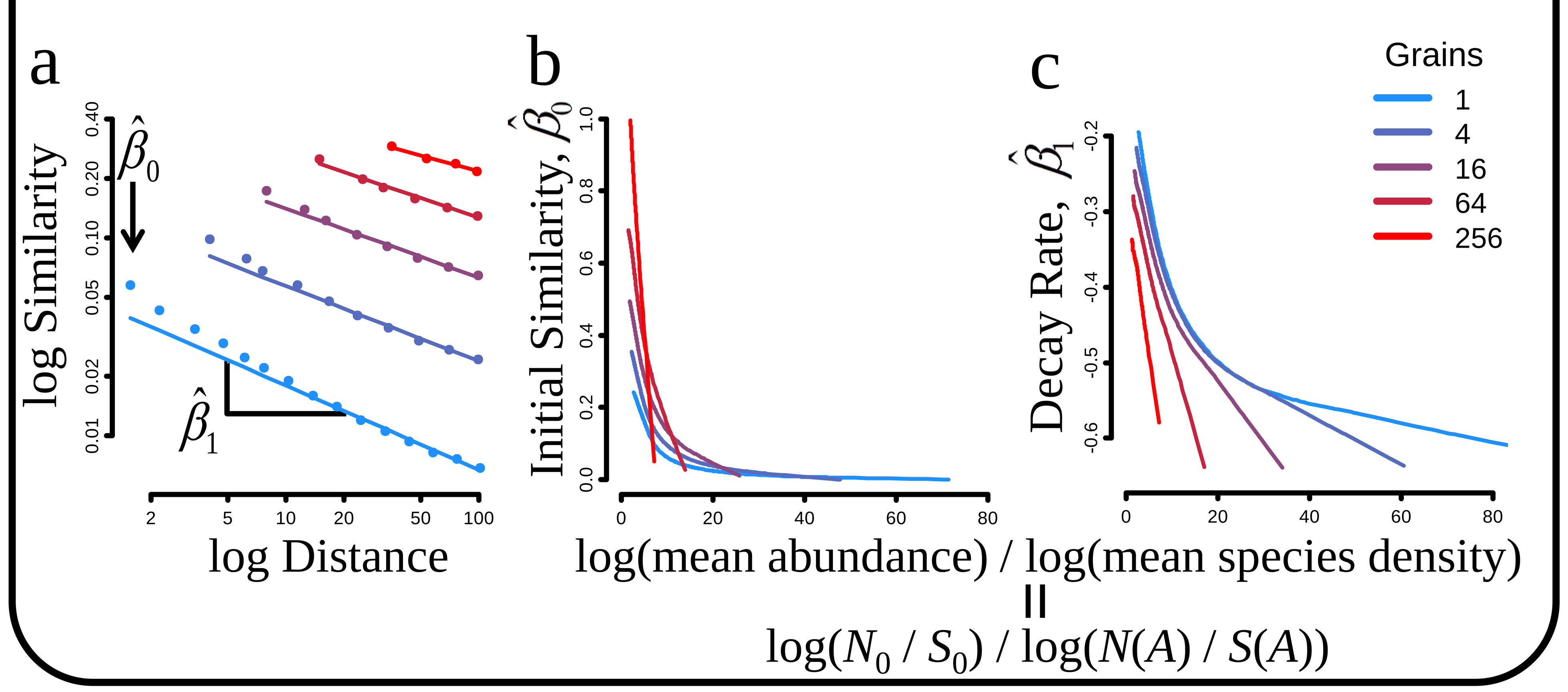
1. **Develop METE's spatially explicit predictions**
2. **Examine the degree of fit to empirical data**
3. **Compare METE's performance to the hypothesis of random placement**



S_0 = # species, N_0 = # individuals, n_i = # individuals of species i

METE Distance Decay

The METE DDR of Sorensen's Similarity index, are well described by a power model (**a**). The intercept $\hat{\beta}_0$ and slope $\hat{\beta}_1$ of the model are controlled by a ratio of N and S (**b**, **c**).

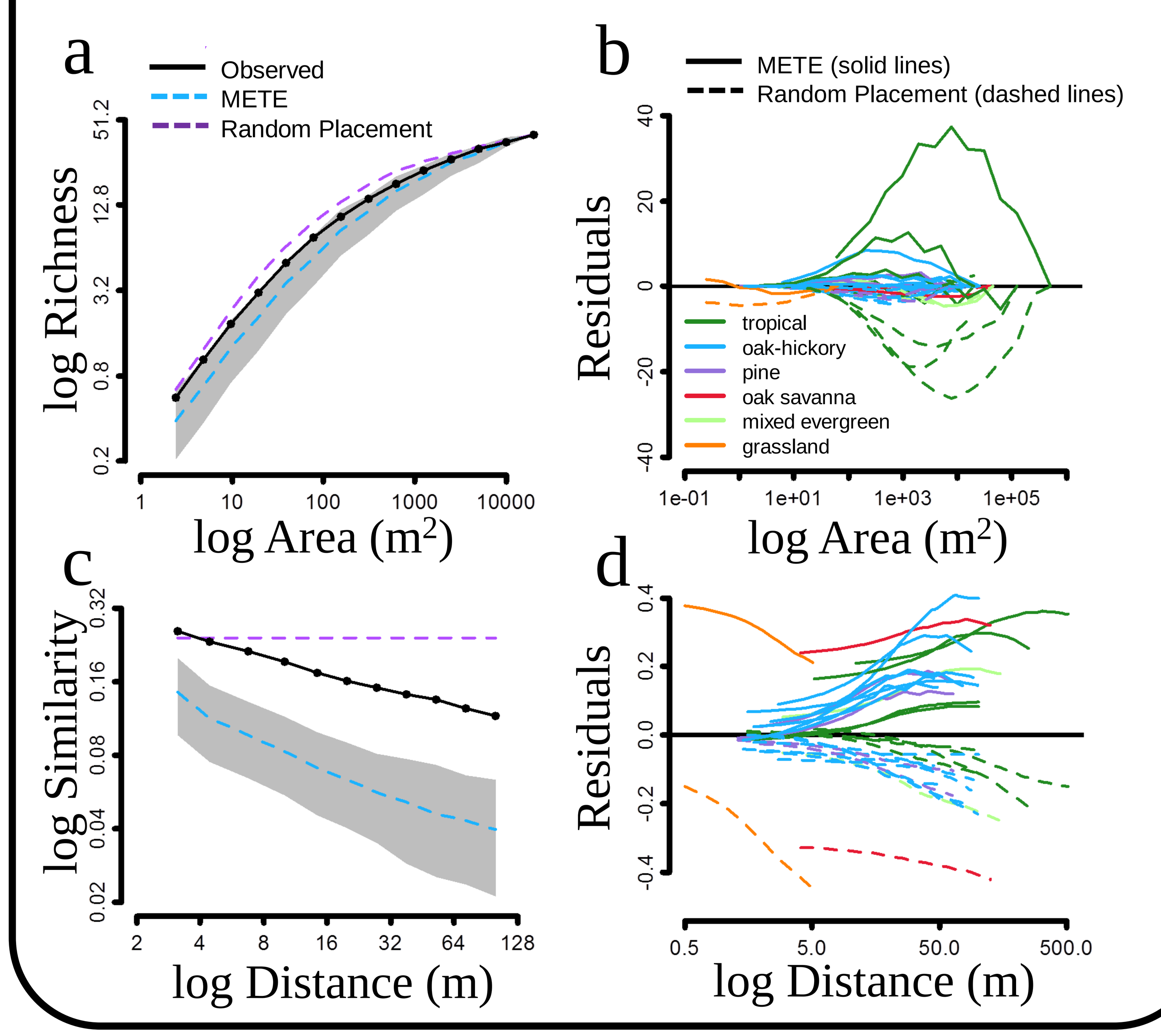


Empirical Datasets

Habitat type	# sites	Extent (ha)	*S*	*N*
tropical forest	4	2.00 – 50	124 – 301	4326 – 205096
oak-hickory forest	7	0.5 – 2.56	17 – 48	669 – 8887
old field pine forest	2	0.85 – 1	36 – 41	2139 – 2584
oak savanna	1	4	7	7625
mixed evergreen forest	1	4.5	31	5885
serpentine grassland	1	0.0064	24	37182
Summary	**16**	**0.0064 – 50**	**7 – 301**	**669 – 205096**

Empirical Results

Panels (**a**, **c**) display typical observed patterns of the SAR and DDR respectively, (**b, d)** display the residuals of the SAR and DDR across all datasets with respect to the METE and random placement models. **Overall the random placement model outperformed METE for both the SAR and DDR**.



Conclusions

We have uncovered that METE predicts a log-log linear pattern of distance decay. The characteristics of the METE DDR are controlled by a ratio of the state variables. METE appeared to capture the functional form of the SAR and DDR, but it fit the data quite poorly. Although overall random placement performed better than METE, it appears that the empirical data may be best described by a middle ground between these two models. Future models should consider a model of intra-specific aggregation that is not random but is less aggregated than METE. The state variable approach, upon which these models are built, provides a simple but powerful framework for unifying community patterns.

Acknowledgements

We thank John Harte for extensive conversations on the use of maximum entropy in ecology. Robert K. Peet provided data for the oak-hickory and old field pine forests. Jessica Green provided data for the serpentine grassland data. José Arévalo provided data for the oak savanna data. The BCI forest dynamics research project was made possible by National Science Foundation grants to Stephen P. Hubbell: DEB-0640386, DEB-0425651,DEB-0346488, DEB-0129874, DEB-00753102, DEB-9909347, DEB-9615226, DEB-9615226, DEB-9405933, DEB-9221033, DEB-9100058, DEB-8906869, DEB-8605042,DEB-8206992, DEB-7922197, support from the Center for Tropical Forest Science, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Small World Institute Fund, and numerous private individuals, and through the hard work of over 100 people from 10 countries over the past two decades. The plot project is part the Center for Tropical Forest Science, a global network of large-scale demographic tree plots. The Luquillo Experimental Forest Long-Term Ecological Research Program, supported by the U.S. National Science Foundation, the University of Puerto Rico, and the International Institute of Tropical Forestry. This research was supported by a CAREER grant from the U.S. National Science Foundation to EPW (DEB-0953694). The USU Ecology Center contributed travel funding.