

**Testing the Maximum Entropy Theory of Ecology for predicting Species Abundance Distributions and Species Area Relationships in Control and Warmed Plots at the Rocky Mountain Biological Laboratory**

Katya Cherukumilli

**ABSTRACT**

The purpose of this study was to test how accurately the Maximum Entropy Theory of Ecology (METE) will predict the Species Area Relationships (SAR) and Species Abundance Distributions (SAD) of plants and SAD of insects in disturbed (warmed) and undisturbed (control) sites in the “Warming Meadow” at the Rocky Mountain Biological Laboratory (RMBL). Based on METE’s prediction that empirical SAR data should fall along a curve known as the “universal scale collapse” curve, I hypothesized that METE would be valid for undisturbed sites and invalid for disturbed sites, an inference supported by past experiments conducted at RMBL. I also expected the empirical plant and insect data for control plots to fit METE’s prediction. Contrary to my hypotheses, statistical analysis indicated that empirical SAR curves for warmed plots (mean distance  $x = .044$ ) lay *closer* to the theoretical curve than the control plots’ curves (mean distance  $x = .106$ ). Similarly, Chi-squared goodness-of-fit test statistics for SAD indicated that for both plants and insects, only one warmed and one control plot showed a significant fit to the theory. Ultimately, the study’s conclusion either indicates a failure of theory or a failure of experimental setup. Possible explanations for why METE appears to predict the SAR and SAD accurately for disturbed and undisturbed plots include the relatively moderate level of warming (2.0°C), a short time period of warming (21 years), or a new species composition equilibrium reached by the ecosystem.

**KEYWORDS**

disturbance, ecosystem, macroecology, biodiversity, climate change

## INTRODUCTION

Since the beginning of the 20<sup>th</sup> century, global surface temperatures have risen 0.8°C, with the majority of warming occurring in the last three decades due to anthropogenic activities like deforestation and fossil fuel use (Hansen et al. 2006). In today's world, climate change is a major threat to the maintenance of biodiversity and ecosystem services. The international scientific community concurs that warming will be of greater magnitude for ecosystems located at higher latitudes and altitudes, with temperature increases between 1.8°C and 4.0°C (Xu et al. 2010, Hofgaard et al. 2010). Post industrialization, there has been a large increase in atmospheric carbon dioxide (CO<sub>2</sub>), a major greenhouse gas that traps reradiated solar radiation, which increases temperature. In addition, exhaustion of storage reservoirs for CO<sub>2</sub> in oceanic and terrestrial (vegetation/soils) sinks may create positive feedback cycles to warming because of excess CO<sub>2</sub> accumulating in the atmosphere. (Barnes & Roy 2010, Hansen et al. 2006). Due to these warming trends, large changes of species distributions in disturbed habitats are likely. Some plant and insect species will move to higher altitudes and latitudes and others may disappear altogether (Jagerbrand et al. 2009). Additionally, Robinet (2010) predicts that warming facilitates the establishment of nonnative invasive species in wider geographical ranges by removing their limiting barriers. To reach an understanding of climate-ecosystem dynamics (e.g., resilience & feedback processes) and the relationship between global warming and natural ecosystems, scientists must carefully maintain long-term climate data records and develop robust macroecological theories that predict natural responses to disturbances (Hansen et al. 2006).

To both qualitatively and quantitatively study the effects of global warming on species distributions in terrestrial ecosystems, numerous scientists have conducted simulated-warming experiments and recorded differences in plant species composition, soil microclimate, and soil carbon levels between warmed and control plots (Wu 2010). The “Warming Meadow” experiment conducted by Harte et al. (1995) at the Rocky Mountain Biological Laboratory for the past two decades has indicated a dramatic shift in plant species composition due to experimental warming: reproductive potential (measured in # of viable flowers produced) of herbaceous flowering species (forbs) has

declined and the growth rate of sagebrush, a drought tolerant and less productive species, has increased (Dunne et. al 2004). Experimental results also show that in warmed plots subject to infrared radiation, soil temperatures have risen by  $\sim 2.0^{\circ}\text{C}$ , soil carbon levels have dropped by 20%, and the snow melt date is approximately 20 days earlier each summer (Harte et. al 2006). These observations indicate that experimental warming has disturbed the local ecosystem. Another warming experiment, known as the “Carbon in Permafrost Experimental Heating Project”, also notes a similar species composition shift from graminoids (grasses and sedges) to shrubs, resulting from permafrost thaw in the Alaskan tundra induced by warming of deep soils by  $1.5^{\circ}\text{C}$  (Natali et al. 2011). Similar to the RMBL experimental setup, Pellini et. al (2011) simulated an ambient temperature increase of  $6^{\circ}\text{C}$  at hardwood forest sites. They recorded the effects of warming on ant and arthropod populations by monitoring population dynamics, species composition, phenology, and behavior of the insects and found that species evenness was highest at intermediate temperatures. Lastly, a Scandinavian study that recorded responses of plant communities before and after simulating a temperature increase showed that graminoids and forbs could be used to monitor ecological changes in alpine meadows (Jagerbrand et. al 2009). Although all of these experimental warming studies clearly indicate that warming serves as a disturbance in plant ecosystems, causing a shift in species composition, scientists have not agreed on an expansive theory to predict the changes in species area and species abundance distributions.

Despite not reaching a consensus, scientists have realized the value and necessity of modeling ecosystem dynamics for future conservation planning as global warming and land-use changes continue to exacerbate biodiversity loss at the landscape scale (Jones 2011). In the past decade, an expansive macroecological theory, known as the Maximum Entropy Theory of Ecology (METE), has been developed to predict community-level variations in ecosystems. In undisturbed ecosystems, METE has been shown to be a reliable tool for predicting Species Area Relationship (SAR), which shows the dependence of species diversity on area, and Species Abundance Distribution (SAD), which shows the spread of individuals of various species in a community of a given area (Harte 2011). In contrast to the previously widely accepted Power Law model that suggests that  $\text{Species} \sim (\text{Area})^z$ , where  $z$  is often taken to be 0.25, METE shows greater

promise for a more accurate estimation of SAR (Rosenzweig 1995). It is important to test METE's power as a predictive tool because this model can allow us to estimate species loss under habitat degradation at a large scale by extrapolating species richness data collected at smaller, more manageable sites (Jones 2011). Although past empirical studies have shown METE's validity in predicting SAR and SAD in undisturbed environments, few have tested whether the theory is valid in disturbed ecosystems and none have tested the theory in a setting where the disturbance is in the form of gradual warming. Thus, this study is necessary for gaining deeper insight into the conditions under which METE might fail to predict accurate SAR and SAD. I am contributing to the field of theoretical ecology by conducting a study on validating METE, which could help conservation biologists determine the ways in which ecosystems respond to disturbances.

The main objective of this study is to test how accurately METE will predict the SAR and SAD of plants and SAD of insects in disturbed and undisturbed sites at the "Warming Meadow" site at RMBL. Based on METE's prediction that empirical SAR data should fall along a curve known as "universal scale collapse", I hypothesize that METE will be valid for the control sites and invalid for warmed sites, an inference supported by past experiments conducted at RMBL (Harte 2011). Additionally, following theory, I expect only my control sites' empirical SAD curves to conform to curves predicted by METE (see theoretical background for details).

### **Theoretical Background for METE**

Originating in the late 50s from the fields of statistical mechanics and information theory, the general Maximum Entropy (MaxEnt) theory is based on a robust mathematical procedure for inferring the least-biased probability distribution given certain constraints. MaxEnt has applications in physics, economics, and computer science (Harte 2011). Professor John Harte developed the Maximum Entropy Theory of Ecology to predict the distribution and abundance of species in various taxonomic groups and across multiple spatial scales. For example, the theory can be used to predict SAD and SAR for ants in the Amazon, rodents in the desert, redwoods in a forest, or even bacteria in the ocean. There are three model inputs for predicting SAR or SAD: the total

ecosystem area ( $A_0$ ), total number of species in  $A_0$  ( $S_0$ ), and the total number of individuals in  $A_0$  ( $N_0$ ). For SAR, an important prediction of METE is that all SAR curves share a common slope at a common value of  $(N)/(S)$  for a given area and that the slope is not constant at 0.25, as the Power Law predicts. For SAD, METE predicts that undisturbed sites should produce a Fisher log-series distribution described by:

$$\Phi(n|S_0, N_0) \approx \frac{1}{\log(\beta^{-1})} \cdot \frac{e^{-\beta n}}{n} \quad (\text{Harte 2011}).$$

METE predicts that disturbed sites will produce a lognormal distribution (Figure 1).

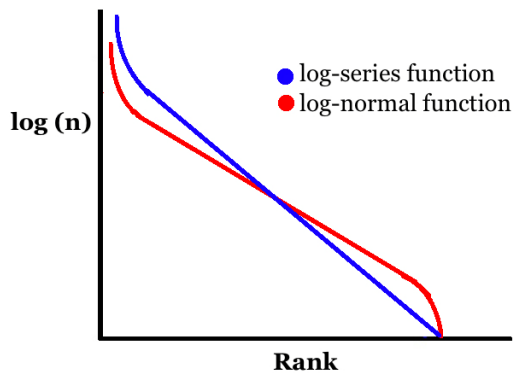


Fig. 1. Theoretical SAD distributions- log-series and lognormal curves

## METHODS

### Experimental system (Harte et. al 2006)

At the Rocky Mountain Biological Laboratory (38.96 N; -106.99 W; elev. 2920m) in Gothic, CO, ten 3x10m plots with 3m of buffer space between adjacent plots were established on undisturbed

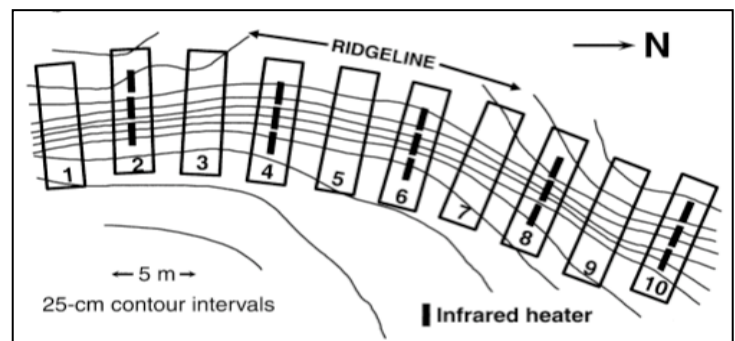
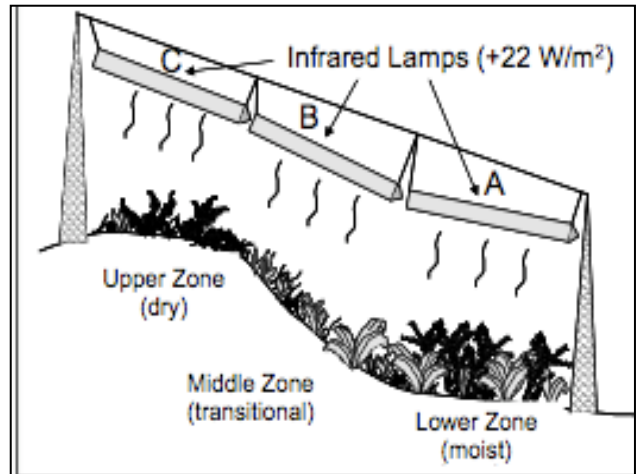


Fig. 2. Layout of 10 plots

terrain known as the “Warming Meadow” in 1989 (Figure 2 from Dunne et. al 2004).

Each plot is sectioned into 3 subplots spanning a 10m microclimate gradient with the driest section, Zone C, at the top and the most moist section, Zone A, at the bottom (Figure 3 from Dunne et. al 2004). Infrared radiators casting a downward heat flux of approximately  $22 \text{ W/m}^2$  have warmed half the plots since 1998, and the remaining 5 plots serve as controls. For the purpose of this study, I collected my plant data from Zone C of Plots 1-6 to have a sample size of



**Fig. 3. Cross-section of a warmed plot**

3 warmed and 3 control plots. I chose Zone C, the driest of all three zones, because it demonstrates the most drastic effects of simulated warming. My insect dataset comes from a census conducted by PI Harte and his graduate students in 1996; it includes species abundance data from over the course of four days in Zone C of Plots 1 through 10. For the SAD analysis portion of this study, I found the average number of individuals and species over the total data collection period and used these cumulative values.

### **Data Collection**

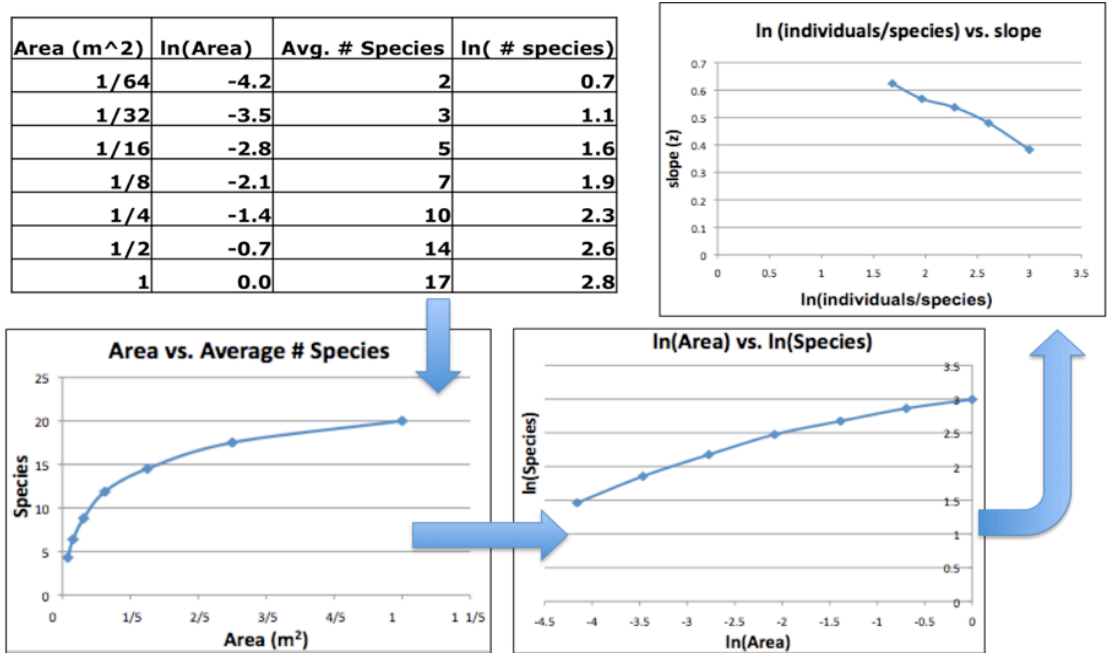
I built a  $1 \times 1 \text{ m}^2$  square quadrat with 8 columns and 8 rows (total 64 cells) to census individuals of plant species in Zone C of Plots 1-6. To ensure that all the living individuals were included in my census, I counted the total number of individuals of all species of forbs, shrubs, and graminoids in each  $1/64 \text{ m}^2$  cell every two weeks during the growing season (June/July). Using an abbreviated code to save space and keep data consistent, I recorded the number and scientific classification of individuals found under each cell of the quadrat (view Appendix A1).

To census the insects for the 1996 dataset, the group used pit traps and counted the number of individuals of each insect species at the end of the day for four consecutive days and recorded the data on excel spreadsheets.

## Data processing

### *Species Area Relationship (plants only)*

In order to find the average number of species present in cells of the areas (in m<sup>2</sup>) 1/64, 1/32, 1/16, 1/8, 1/4, 1/2, and 1, I input the census data recorded for each plot into separate Excel spreadsheets and created presence-absence matrices for each species by representing absence of individuals with a “0” and presence with a “1” (view Appendix A1 & B1). By summing all the presence-absence matrices for each species found in each plot, I calculated the average number of species present in each of the chosen cell areas for consideration. Using this data, I plotted the graphs for each plot with ln(Area) on the x-axis and ln(Species) on the y-axis. I found the values of the local slopes at areas 1/32, 1/16, 1/8, 1/4, and 1/2 m<sup>2</sup> and created the final empirical SAR graphs for each plot by graphing the local slopes against the ln(expected # individuals/species) at each value of area (Figure 4). I calculated the expected number of individuals for each area by multiplying the total number of individuals for that plot by the area (view Appendix B2). I compared these empirical graphs to the universal scale collapse curve predicted by METE.



**Fig. 4. Plotting SAR curves.** First the area vs. species curve was transformed onto natural log space. Then, the local slopes at the points for areas 1/32 through 1/2 were plotted against the natural log of individuals/species.

*Species Abundance Distribution (plants & insects)*

To create the empirical SAD graphs (plots 1-6 for plants and plots 1-10 for insects), I ranked the species in the collected census in order of abundance and at each observed “N” value (e.g., 1,2,3...N=total # individuals in plot), I recorded the fraction of total species with individuals less than or equal to that value of N. Doing this produced cumulative probabilities for the observed data. I then calculated the predicted cumulative probabilities by summing the normalized  $\phi$  values calculated from the log-series formula given by METE (Figure 1,  $\beta$  values derived from total S & N). I plotted the predicted cumulative probability against the observed cumulative probability and compared the line-of best fit of those data points to the  $y=x$  line, which represents the case where the observed data exactly fits the predicted distribution.



## Analysis

### *Checking Empirical Results Against METE Predictions*

To analyze the effectiveness of the Maximum Entropy Theory of Ecology in predicting the SAR, I used the R program (R Development Core 2011) to calculate the distance between the observed and theoretical curves for both the warmed and control plots. Comparing the points on the observed empirical graphs to METE's theoretical curves allowed me to determine the deviation of control vs. warmed plots from METE's predictions.

To assess the effectiveness of METE in predicting SAD for the plants and insects datasets, I used a Chi-squared goodness-of-fit test with 2 degrees of freedom and determined the significance of the empirical data's fit to the theory's predictions (view Appendix C1).

## RESULTS

### *Species Area Relationship (plants only)*

When plotted against the theoretical universal scale collapse curve, the empirical SAR data for both control and warmed plots appear to align closely with METE's predictions (Figure 5). Statistical analysis surprisingly indicates that the warmed plots empirical curves (mean distance  $x = .044$ ) actually lie *closer* to the theoretical curve than the control plots' curves (mean distance  $x = .106$ ) (Figure 6).

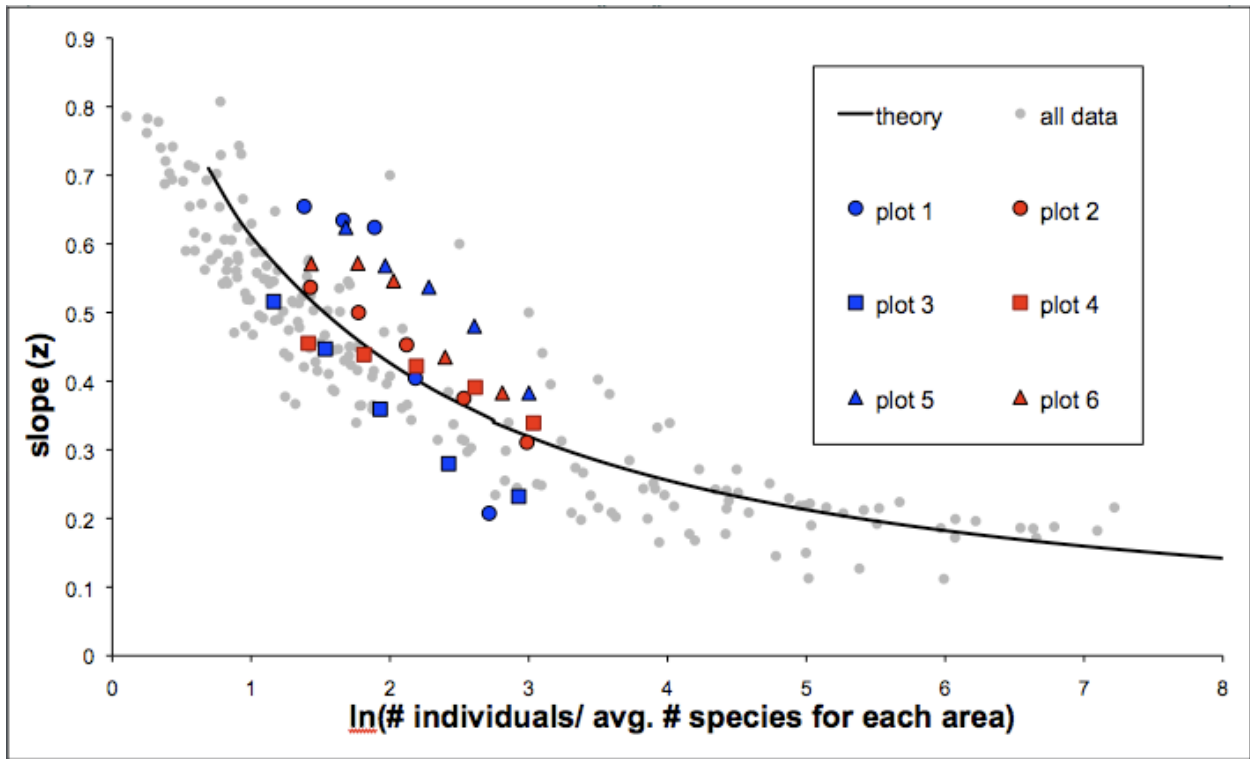


Fig. 5. SAR curves for the control and warmed plots 1-6. All previous experimental data are shown against the theoretical curve predicted by METE, which is in black.

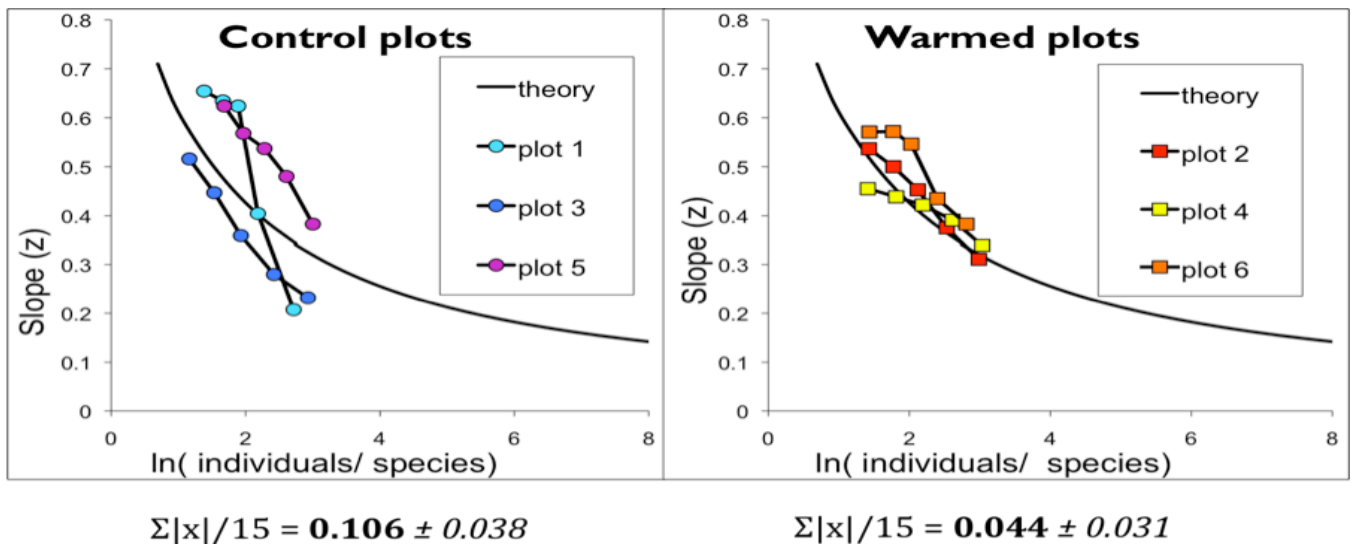
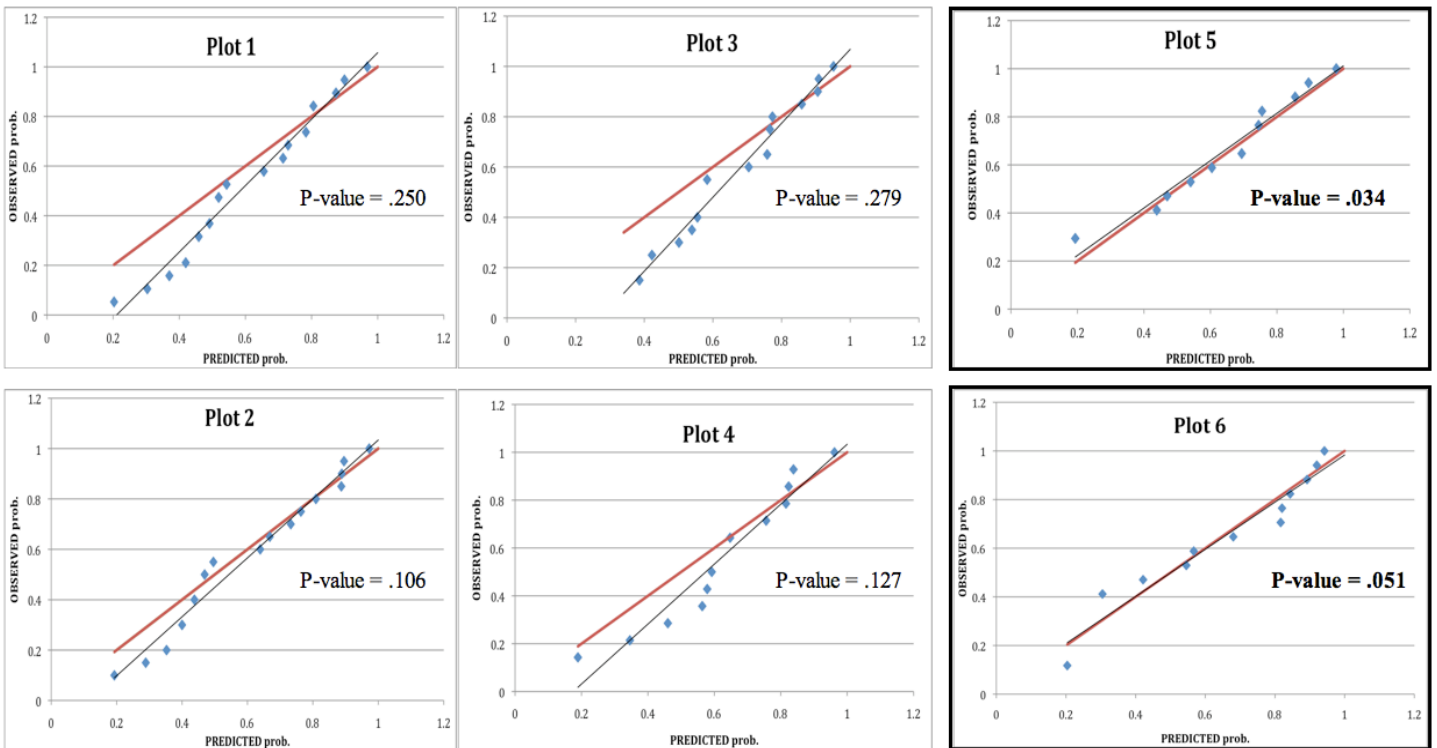


Fig. 6. Average distance of observed data points to theoretical curve for the control and warmed plots. The warmed plots had a lower mean distance and standard deviation than the control plots.

*Species Abundance Distribution (plants & insects)*

For plants, the predicted versus observed cumulative probability SAD plots indicate that the empirical curves appear to be closer to the theoretical curves for some plots and further for other plots, without a noticeable correlation among either the warmed or control plots (Figure 7). The Chi-squared goodness-of-fit test indicates that Plot 5 (a control plot) and Plot 6 (a disturbed warmed plot) were the only plots with significant p-values, of 0.034 and 0.051 respectively.

For insects, the Chi-squared goodness-of-fit test indicates that Plot 6 (a disturbed warmed plot) and Plot 7 (a control plot) were the only plots with significant p-values, of 0.043 and 0.048 respectively (Figure 8).



**Fig. 7. Plant SAD plots for Plots 1 through 6.** The red line shows  $y=x$ , where predicted probability=observed probability. The blue dots and their corresponding black linear regression line are the empirical cumulative probabilities. The plots outlined in black had significant p-values ( $p < \text{about } 0.05$ ).

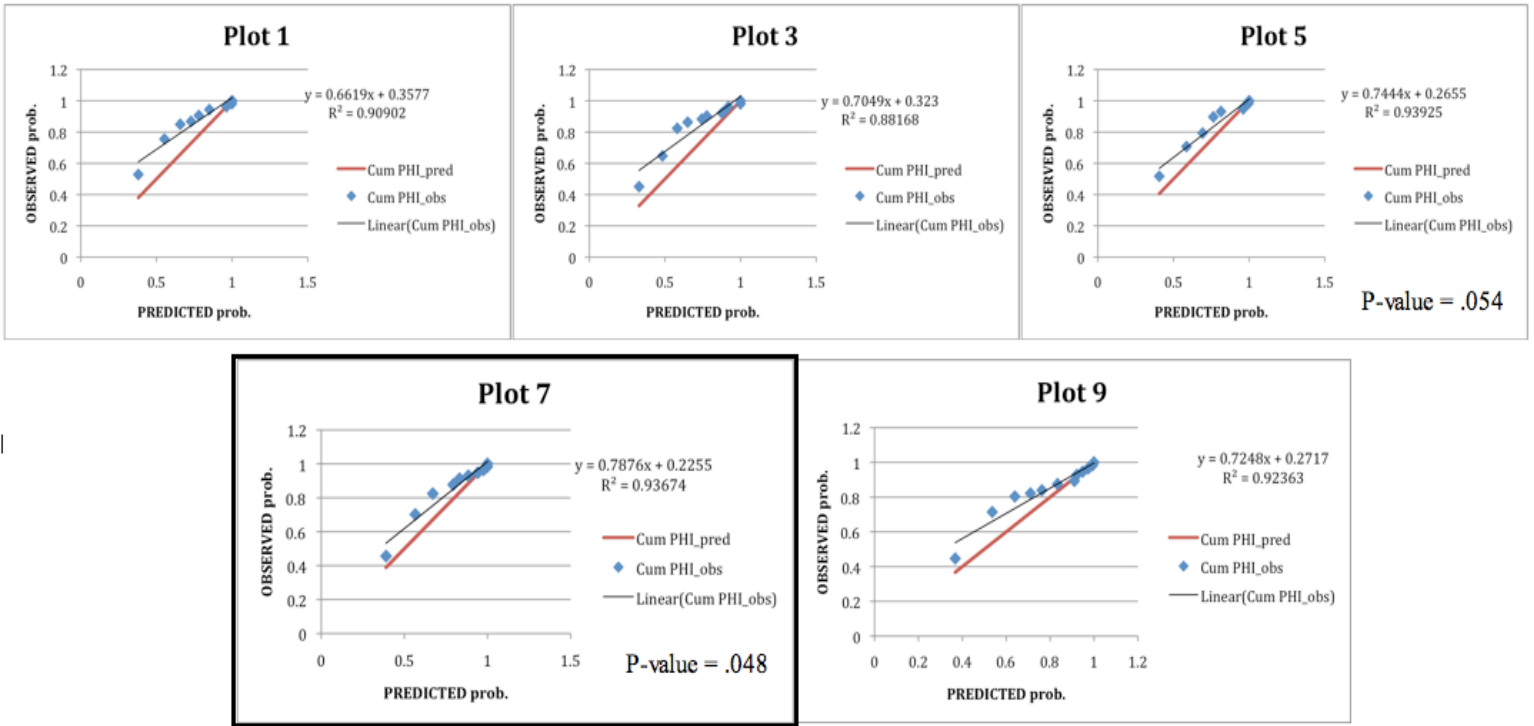


Fig. 8. Insect SAD plots for control plots (1,3,5,7,9). Plot 7 has a significant p-value.

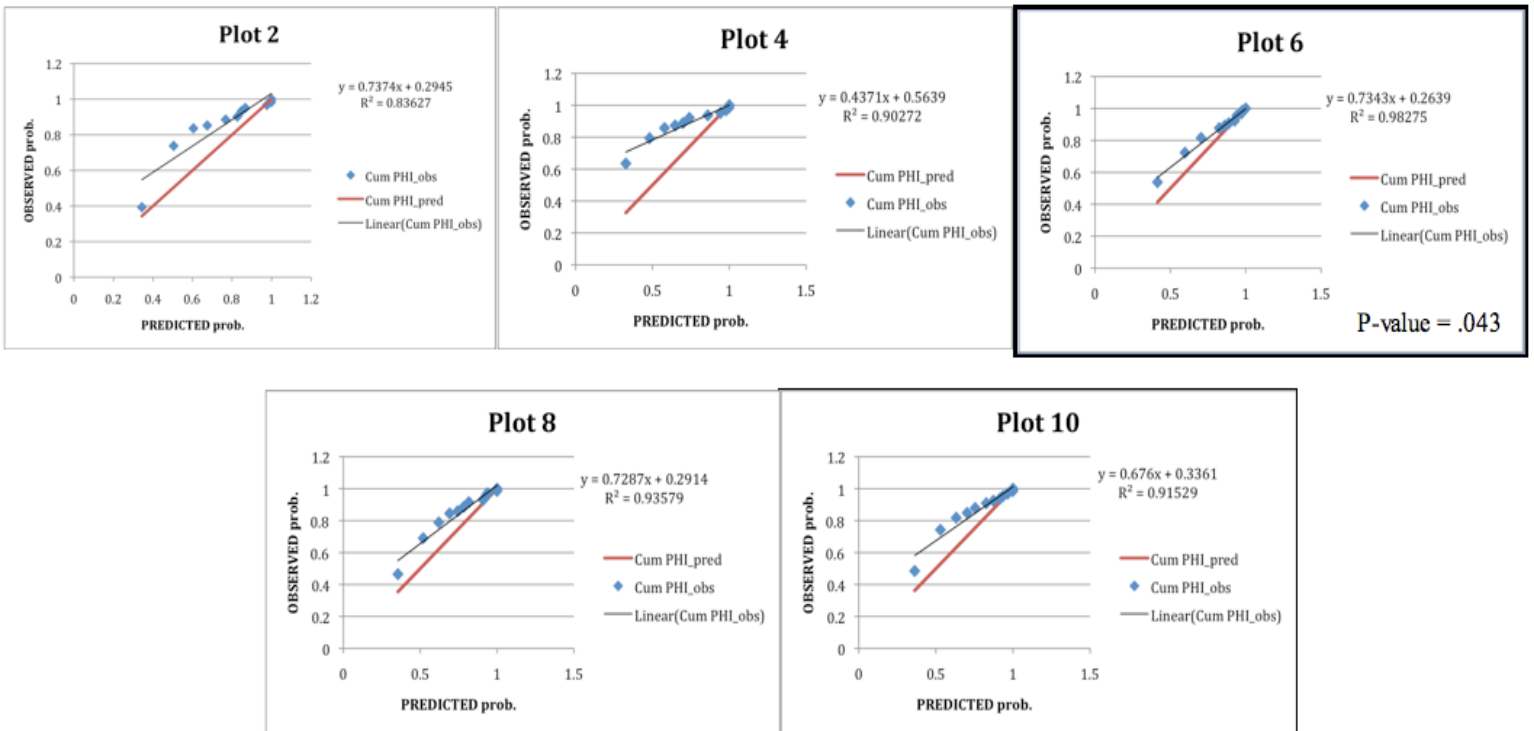


Fig.9. Insect SAD plots for warmed plots (2,4,6,8, 10). Plot 6 has a significant p-value

## DISCUSSION

The objective of this study was to test to robustness of the Maximum Entropy Theory of Ecology (METE) at predicting the Species Area Relationships (SAR) and Species Abundance Distributions (SAD) for plants and insects in warmed and control sites at the Rocky Mountain Biological Laboratory's (RMBL) Warming Meadow. For undisturbed sites, I hypothesized that METE would accurately predict the SAR and SAD, with empirical curves falling on the universal scale collapse curve or a Fischer log-series distribution respectively, and that the theory would fail for the disturbed warmed sites.

### **Empirical Results vs. METE Predictions**

My observational study produced unanticipated findings: the plant SAR curves showed compliance with METE for all warmed and control plots and the plant/insect SAD curves only complied with METE for plots 5 & 6. Based on the results, my hypotheses that METE would be valid at predicting SAD and SAR for control undisturbed plots and would fail for the warmed plots appears to be false. Overall, the results show that in some cases METE can accurately predict distributions for warmed and control plots and in other cases the theory it doesn't work for either. The results for SAR indicate no difference in METE's ability to predict for control vs. treatment plots and the results for SAD do not support METE. In particular, the SAR graphs from the empirical plant data fell along the universal scale collapse curve predicted by METE, without a distinguishable difference between warmed and control plots. In fact, statistical analysis indicated that the warmed plots' SAR curves fell slightly closer to the scale-collapse curve than the undisturbed control plots. In contrast, the SAD plant and insect data plotted against the theoretical METE curves indicated that the theory was accurate only for plots 5 & 6 and plots 6 & 7 respectively, which seems surprising because plot 5 & 7 are controls and plot 6 is warmed. Ultimately, the rejection of the original hypothesis might indicate a failure of theory or a failure of experimental setup. Comparing METE to other theories, analyzing how insects and plants respond to disturbances like warming,

and looking at potential limitations of my study can help explain the significance of these results.

### **Comparing METE to Other Theories**

My SAR results indicated that the METE was relatively successful in predicting the plants SAR for *both* disturbed and undisturbed sites. This finding contradicts previous SAR data predicted by the Power Law, which appears to fail completely in disturbed settings (May 2000). My results for the SAD tests don't agree with Ronald Fischer's study, which tested and validated the power of the log-series function in predicting the SAD of agricultural plants disturbed by pests (Fisher 1943). Robert May and Brian McGill present other theories to describe SAD and argue that sampling and scale greatly influence the shape of SAD curves (McGill 2007). These studies indicate that my ambiguous conclusions may be due to an inadequate sample size (i.e., quadrat area was too small).

### **How do insects react to warming?**

Expanding the interpretation of results in the larger context of organisms' responses to climate change can help shed light on the significance of this study's conclusions. The biological impact of anthropogenic climate change strongly depends on the temperature sensitivity and latitudinal location of terrestrial organisms (Deutsch et. al 2008). Insects are ectothermic (i.e. depend on external sources for body heat) and are thus highly sensitive to fluctuating ambient temperatures (Robinet 2010). Past research indicates that tropical insects are most sensitive to temperature change and insects at higher latitudes may have enhanced fitness in spite of warming due to their expanded range of thermal tolerance. Since RMBL is considered to be a "high latitude" site, the insects in our dataset may have a larger thermal tolerance range, a fact that should be taken into account when interpreting the conclusions. Others argue that the microhabitats where insects live, insects' adaptation mechanisms to local climates, and their overall thermal sensitivity greatly depends on their life stage; higher temperatures may prevent

survival of organisms to maturity (Kingsolver et. al 2011). Alternately, because most insect herbivores have their primary growth period during the warmer parts of year, changing the temperature range can accelerate the development of the insects during their growth phases (Bale et. al 2002). Robinet (2010) found that the effects of climate change on insects could differ seasonally and spatially, and that warming could allow insects to survive in the winter, have earlier flight periods, and develop quicker (Robinet 2010). Thus, gradual warming at RMBL may have affected the growth and development of the insect populations, which could explain the abnormal SAD data.

### **Limitations**

The inferences that can be drawn from this study are limited by the experimental setup and other confounding factors. The biggest limitation of this study is the small sample size. For the plants dataset, I could only sample the upper Zone C of Plots 1-6, which allowed me to have 3 disturbed and 3 undisturbed plots; but a larger area (or quadrat) size might have produced clearer trends in the results. Another reason for the unanticipated results might be that people trampling on the plots in past years could have also disturbed the control plots, which are assumed to be undisturbed. In other words, perhaps our control group was not well representative of a pristine environment.

### **Broader Implications**

Ultimately, gaining deeper understanding of patterns of species abundance and distribution can be an important tool for conservation biologists to protect species in the face of current climate change. Developing robust theories like METE can help predict the most common and rare species in an ecosystem and the effects of habitat loss on species abundance and diversity. Making these predictions for larger habitats by extrapolating and scaling up from smaller data sets is valuable because it is too time intensive for conservation biologists to collect a comprehensive dataset describe an entire ecosystem's characteristics.

My study points to one of two broader implications, depending on the interpretation of the results: 1) it is important to rethink the ability of METE in predicting SAR and SAD for both control and disturbed sites (i.e. it works for both), or perhaps 2) it is necessary to conduct further research on what can be defined as a true disturbance for a given ecosystem. Possible explanations for why METE appears to predict the SAR and SAD accurately for disturbed and undisturbed plots include the relatively moderate level of warming (2.0°C), a short time period of warming (21 years), or a new species composition equilibrium reached by the ecosystem.

### **Future Directions**

Future students continuing this project should look at the correlation of other factors (e.g. plots' moisture levels, snowmelt dates, soil carbon levels, and plant species composition) with the compliance of SAR and SAD curves to METE to better understand this study's conclusions on the predictive power of the theory. Additional work in the field of theoretical macroecology could focus on further categorizing disturbances so climate change and gradual warming can be better contextualized among other disturbances. To do this, researchers should record the effects of sudden disturbances versus slow changes over time to understand whether the rate of change or the magnitude of disturbance matters more in ecosystem dynamics. Some authors claim, "it is not the magnitude of change that is important, but the unpredictability in the system"; so future projects could treat disturbances as stochastic environmental conditions rather than as systemized simulated warming (Bale et. al 2002). Lastly, we should try to understand the impacts of analyzing data over space and time on METE's predictions of SAR and SAD and try to develop a theory that can predict the evolution of species area and abundance distributions over time.

### **ACKNOWLEDGEMENTS**

I am so grateful for the help of my wonderful mentor, Professor John Harte. Throughout the entire research process, from field collection at RMBL to compiling the final thesis,



he answered countless questions to help deepen my understanding of the subject. I appreciate the help of Tess Leuthner for her countless hours of work during the data collection period of this project and Mel Harte for helping us identify the wildflower species. Many thanks go out to Melissa Eitzel for helping me conduct statistical tests, CNR's ES program for structuring our research progress and thesis compilation, and friends & family for their support throughout the whole process. I could not have completed this project without the assistance of the Haas scholarship, which funded my travel and stay at RMBL.

## REFERENCES

- Bale J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1-16.
- Barnes, C. A. and D. P. Roy. 2010. Radiative forcing over the conterminous United States due to contemporary land cover land use change and sensitivity to snow and interannual albedo variability. *Journal of Geophysical Research-Biogeosciences* **115**: [doi:10.1029/2010JG001428 ].
- Deutsch C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105:6668-6672.
- Dunne J. A., S. R. Saleska, M. L. Fischer, and J. Harte. 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* 85: 904-916.
- Fisher R. A., A. S. Corbet, and C. B. Williams. 1943. The Relation Between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population. *Journal of Animal Ecology* 12: 42-58.
- Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medinaelizade. 2006. Global temperature change. *Proceedings of the National Academies of Sciences* 103: 14288-14293.
- Harte, J. February 1995. Global Warming and Soil Microclimate: Results from a Meadow-warming Experiment. *Ecological Applications* 5: 132-150.

- Harte, J. June 2011. *Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and Energetics*. Oxford University Press, NYC, New York, USA.
- Harte, J., S. Saleska, and T. Shih. 2006. Shifts in plant dominance control carbon-cycle responses to experimental warming and widespread drought. *Environmental Research Letters* 1: [doi: 10.1088/1748-9326/1/1/014001].
- Hofgaard A., J. O. Lokken, L. Dalen, and H. Hytteborn. 2010. Comparing warming and grazing effects on birch growth in an alpine environment - a 10-year experiment. *Plant Ecology & Diversity* 3:19-27.
- Jagerbrand A. K., J. M. Alatalo, D. Chrimes, and U. Molau. 2009. Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia (Berlin)* 161:601-610.
- Jones J. P. G. 2011. Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* 48:9-13.
- Kingsolver J. G., H. A. Woods, L. B. Buckley, K. A. Potter, H. J. MacLean, and J. K. Higgins. 2011. Complex Life Cycles and the Responses of Insects to Climate Change. *Integrative and Comparative Biology* 51:719-732.
- May R. M., M. P. H. Stump. 2000. Species-area relations in tropical forests. *Science (Washington D C)* 290:2084-2086.
- McGill B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J. Enquist, J. L. Green, F. He, A. H. Hurlbert, A. E. Magurran, P. A. Marquet, B. A. Maurer, A. Ostling, C. U. Soykan, K. I. Ugland, and E. P. White. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10:995-1015.
- Natali S. M., E. A. G. Schuur, C. Trucco, C. E. H. Pries, K. G. Crummer, and A. F. B. Lopez. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biology* 17:1394-1407.
- Pelini S. L., F. P. Bowles, A. M. Ellison, N. J. Gotelli, N. J. Sanders, and R. R. Dunn. 2011. Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution* 2:534-540.
- R Development Core Team. 2011: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robinet C., A. Roques. 2010. Direct impacts of recent climate warming on insect populations. *Integrative Zoology* 5:132-142.

- Rosenzweig M. L. 2004. Applying species-area relationships to the conservation of species diversity. Pages 325-343 *In* M. H. Lomolino LR, editor. *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer Association, Sunderland, Massachusetts, USA.
- Wu, Z., P. Dijkstra, G.W. Koch, J. Peñuelas, and B.A. Hungate. 2010. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* 17: 927-942.
- Xu Z., R. Hu, P. Xiong, C. Wan, G. Cao, and Q. Liu. 2010. Initial soil responses to experimental warming in two contrasting forest ecosystems, Eastern Tibetan Plateau, China: Nutrient availabilities, microbial properties and enzyme activities. *Applied Soil Ecology* 46:291-299



**APPENDIX B: SAR**

B1. Formula for making presence/absence matrices: On Excel, I wrote “If (cell A1>0, 1,0)”. This states that if the particular cell A1 has at least one or more individuals in it, then a 1 should indicate the presence of that species in that cell (as opposed to a 0, which indicates an absence).

B2. Example demonstrating the calculation for expected number of individuals: For  $A=1/2 \text{ m}^2$ , the expected # individuals in Plot 1 with a total of 506 individuals was  $506/2=253$  individuals. For  $A=1/8 \text{ m}^2$ , the expected # individuals in Plot 1 with a total of 506 individuals was  $506/8=63.25$  individuals (for the purpose data analysis and plotting empirical curves, the decimal does not pose a problem).

APPENDIX C: SAD

	B	C	D	E	F	G	H	I	J
1	$\Phi(n)$	norm( $\Phi(n)$ )	$S_0 * \text{SUM}(1:n)$	$S_0 * \text{SUM}(1:n)$	Cum PHI_pred	Cum PHI_obs	Cum PHI_obs	Cum PHI_pred	chi^2 value:
2	0.917686	0.36748392	20.57909949	20.57909949	0.367483919	0.446428571	0.446428571	0.367483919	0.01695927
3	0.42107379	0.16861742	30.02167519	30.02167519	0.536101343	0.714285714	0.714285714	0.536101343	0.05922326
4	0.25760902	0.10315857	35.79855484	35.79855484	0.639259908	0.803571429	0.803571429	0.639259908	0.04223364
5	0.17730314	0.07100038	39.774576	39.774576	0.710260286	0.821428571	0.821428571	0.710260286	0.0173998
6	0.13016689	0.05212484	42.69356715	42.69356715	0.762385128	0.839285714	0.839285714	0.762385128	0.00775684
7	0.09954361	0.03986186	44.92583157	44.92583157	0.802246992		0.875	0.833601857	0.00205591
8	0.07829981	0.03135486	46.68170396	46.68170396	0.833601857	0.875	0.892857143	0.910429894	0.00033918
9	0.06287281	0.02517718	48.09162603	48.09162603	0.858779036		0.928571429	0.922333876	4.2183E-05
10	0.05128666	0.02053755	49.24172891	49.24172891	0.879316588		0.946428571	0.94837023	3.9753E-06
11	0.04235855	0.01696232	50.19161888	50.19161888	0.896278909		0.964285714	0.972624038	7.1485E-05
12	0.03533804	0.01415099	50.98407408	50.98407408	0.910429894	0.892857143	0.982142857	0.992380929	0.00010562
13	0.02972679	0.01190398	51.65069704	51.65069704	0.922333876	0.928571429	1	0.999453867	2.9842E-07
14	0.02518141	0.0100838	52.21538985	52.21538985	0.932417676				0.14619147
15	0.02145801	0.00859278	52.69658549	52.69658549	0.941010455				
16	0.01837893	0.00735977	53.10873289	53.10873289	0.94837023	0.946428571			
17	0.01581196	0.00633184	53.46331592	53.46331592	0.95470207				
18	0.01365686	0.00546884	53.76957087	53.76957087	0.960170908				
19	0.01183645	0.00473986	54.03500308	54.03500308	0.964910769				
20	0.01029045	0.00412077	54.26576633	54.26576633	0.969031542				
21	0.00897123	0.0035925	54.46694611	54.46694611	0.972624038	0.964285714			
22	0.00784074	0.00313979	54.64277457	54.64277457	0.975763832				
23	0.00686827	0.00275037	54.79679554	54.79679554	0.978514206				
24	0.00602888	0.00241424	54.93199309	54.93199309	0.980928448				
25	0.00530209	0.0021232	55.05089245	55.05089245	0.983051651				
26	0.00467103	0.0018705	55.15564024	55.15564024	0.984922147				
27	0.00412167	0.00165051	55.24806868	55.24806868	0.986572655				
28	0.00364231	0.00145855	55.32974747	55.32974747	0.988031205				
29	0.00322312	0.00129069	55.40202597	55.40202597	0.989321892				
30	0.00285582	0.0011436	55.46606773	55.46606773	0.990465495				
31	0.00253339	0.00101449	55.52287896	55.52287896	0.991479981				
32	0.00224986	0.00090095	55.57333205	55.57333205	0.992380929	0.982142857			
33	0.00200014	0.00080095	55.61818527	55.61818527	0.99318188				
34	0.00177988	0.00071275	55.65809913	55.65809913	0.993894627				
35	0.00158533	0.00063484	55.69365022	55.69365022	0.994529468				
36	0.00141327	0.00056594	55.72534281	55.72534281	0.995095407				
37	0.00126091	0.00050493	55.75361878	55.75361878	0.995600335				
38	0.00112585	0.00045084	55.77886594	55.77886594	0.996051177				
39	0.00100599	0.00040284	55.80142518	55.80142518	0.996454021				
40	0.00089951	0.0003602	55.82159666	55.82159666	0.996814226				
41	0.00080483	0.00032229	55.83964497	55.83964497	0.997136517				
42	0.00072057	0.00028855	55.85580368	55.85580368	0.997425066				
43	0.00064551	0.00025849	55.87027924	55.87027924	0.997683558				
44	0.0005786	0.0002317	55.88325432	55.88325432	0.997915256				
45	0.00051891	0.00020779	55.89489076	55.89489076	0.998123049				
46	0.00046561	0.00018645	55.90533206	55.90533206	0.998309501				
47	0.00041799	0.00016738	55.91470559	55.91470559	0.998476886				
48	0.00037543	0.00015034	55.92312453	55.92312453	0.998627224				
49	0.00033735	0.00013509	55.93068951	55.93068951	0.998762313				

**Figure C1: Screenshot of excel spreadsheet-showing data used to create empirical and theoretical SAD curves for insects and plants. First,  $\phi(n)$  was calculated using the log-series formula, then these values were normalized, multiplied by the # species, and cumulatively summed. These cumulative predicted probabilities were plotted against the cumulative observed probabilities, which were calculated by recording the fraction of total species with individuals less than or equal to that value of N. Chi-squared values were calculated to test significance of fit between empirical data and predictions.**