

Testing the Maximum Entropy Theory of Ecology in the Warming Meadow

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Abstract

As global climate change responses are increasingly observed, theories in macroecology are being tested in order to up-scale species richness data to estimate extinction rates under habitat loss or degradation due to land use and climate change. Insight into effects that anthropogenic warming can have on subalpine meadow ecosystems has been of increasing interest and is the site used for this study of a macroecological theory. Over the past 21 years, many observational changes as a result of heating have been measured in the Rocky Mountain Biological Laboratory Warming Meadow. It is thought that the heated meadows are a disturbed ecosystem due to the responses to earlier snowmelt date such as changes in soil microclimate, flowering phenology, plant species composition, and soil organic carbon levels. To test the validity of the Maximum Entropy Theory of Ecology (METE) in disturbed and undisturbed sites, we calculated species area relationships (SARs) and species abundance distributions (SADs) for six plots. It was predicted that because there is evidence that the theory may fail in disturbed sites, that the heated plot SARs and SADs would not follow the predictions of METE. Contrary to our hypotheses, both the control and heated plots followed predictions made by the theory for both SAR and SAD. Possible conclusions are either that the heated plots may not yet be disturbed, the plots may already be adapted, or the theory may predict for disturbed as well as undisturbed sites.

Introduction

To have the ability to predict the direction and magnitude of responses to global climate change (as well as other disturbances) is of increasing importance in ecology and climate change policy (IPCC). Interest has grown in testing macroecological theory that could potentially answer such questions by predicting species richness of an area for census data and conservation purposes, providing knowledge of responses to the change or loss of habitat. For example, insight into effects that anthropogenic warming can have on subalpine meadow ecosystems has been of increasing interest and is the site used for this study of a macroecological theory.

For the past two decades at Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado a warming experiment has been conducted in a subalpine meadow. Data have been collected regarding responses to climate change that have been observed. For example, as a

result to earlier snowmelt in heated plots, changes have been observed in soil microclimate (changes in moisture and temperature levels) (Harte et al. 1995), flowering phenology (Dunne et al. 2003), plant species composition (Harte and Shaw, 1995; Perfors et al., 2003; Harte et al., 2006; Cross et al. 2007), and levels of soil organic carbon (SOC) (Saleska et al. 2002) in response to experimental warming.

The RMBL warming meadow experimental facility will be used to test a theory that predicts the form of species abundance distributions (SADs) and species area relationships (SARs). Knowledge of the form of the SAR and the SAD provides invaluable knowledge to conservation biologists, because these metrics are used to estimate species richness at spatial scales too large to census directly (Harte et al., 2009) and to estimate species loss under climate change and habitat degradation from human land use (Thomas et al., 2004). A more reliable prediction of area relationship and species abundance is predicted in this theory.

The theory to be tested is the Maximum Entropy Theory of Ecology (METE) developed by Harte and co-workers over the past four years. A detailed exposition of the background and development of the theory can be found in Harte (2011) and specific predictions are described in Harte et al. (2008; 2009). Overall, the Maximum Entropy Theory of Ecology predicts the distribution, abundance, and energetics of species across multiple spatial scales and taxonomic groups (Harte, 2011). The theory assumes prior knowledge of a small set of state variables: the area of the ecosystem, A , the total number of species in the system, S , the total number of individuals in the species, N , and the total metabolic rate of the individuals, E (Harte et al. 2009). METE is a mathematical procedure for inferring least-biased probability distributions, while incorporating prior knowledge (or constraints) that arise from knowledge of the state variables.

Traditionally, the species area relationship is plotted as $\log(\text{species richness})$ versus $\log(\text{area})$. Analysis of such plots indicates that the shape of the SAR depends significantly on the scale of analysis, the type of habitat, and the taxa being studied (Rosenzweig, 1995; Drakare et al., 2006; Harte et al., 2009). However, METE predicts a universal scale-collapse curve for the SAR (Figure 2) (Harte et al. 2009). The slope of the species area relationship predicted by METE will be a specified and universal function of $\log(N/S)$ instead of following a horizontal line as predicted by the power law model: $S(A) = cA^z$. The theory is tolerant of taxonomic confusion as long as the units of analysis are consistent within and across all plots.

The prediction of species abundance distributions by METE results in a Fisher log series (Harte 2008). While this form of the SAD is frequently observed in census data, it has been observed that in heavily disturbed ecosystems the SAD tends to be better described by the lognormal distribution (Kempton and Taylor, 1978; Harte 2011).

In particular, this experiment provided the opportunity to test the validity of METE predictions under both undisturbed (control plots) and disturbed (heated plots) conditions in the same ecosystem. This is important because while most tests of the theory have been carried out in relatively undisturbed systems, there is some evidence (Harte 2011) that the theory's predictions fail in relatively disturbed systems.

We hypothesized that:

1. The slopes of the SARs plotted against $\log(N/S)$ will follow the predicted universal curve in control plots and will not in the heated plots.
2. A logseries SAD will be observed in the control plots and a lognormal SAD in the heated plots.

Methods

The study site was located in the Research Meadow at the Rocky Mountain Biological Laboratory in Gothic, Colorado. In the summers of 1989 and 1990, ten 3 by 10 meter plots were set up with each plot spanning a moisture gradient in its long dimension. Adjacent plots are separated by approximately three meters. Each plot was sectioned into a lower, middle, and upper zone (A, B, and C respectively) to account for the variations in soil moisture and vegetation along the slope (Harte et al. 1995). The plots alternate control and heated along a glacial moraine.

The experimental plots are warmed with infrared radiation from three electric heaters that are approximately 1.2 m above ground and add 22 W/m^2 of IR flux (Figure 1). In the treatment plots the soil temperature has risen on average 2 degrees Celsius relative to control plots and snow melts approximately two weeks earlier than control plots (Harte et al. 1995; 2002).

In this study, we constructed from census data a species area relationship (SAR) and a species abundance distribution (SAD) for a 1m x 1m subplot in the upper zone C in treatment and control plots 1-6. We counted the number of individuals of each species of forbs, shrubs, and graminoids in each 1/8m x 1/8m cell. This was done three times for each plot (about once every two weeks) throughout the summer.

The data from heated and control plots were analyzed by first plotting $\log(S)$ against $\log(A)$, and then plotting the local slopes of that empirical curve against $\log(N/S)$ at each value of area for which there are species richness data to create the SAR. We used GNU R to

calculate the distance between the warming

meadow data sets and the theoretical curve were

then calculated to determine the deviation of the control versus treated plots from the curve.

Using the previous data points, five points were randomly selected to generate a mean deviation from the theoretical curve in order to simulate selecting for the five points per plot of the warming meadow data. This was run 10,000 times to create a histogram of the frequency of where the previous data points lie in relation to the theoretical curve. With this histogram, a p-value was then calculated to determine the probability that the warming meadow data from this study had a greater deviation from the theory than the previous data set deviation.

The SAD data was analyzed by ranking the species in order of abundance to determine the rank-abundance curve, which allows discrimination between the log series and the lognormal distribution.

Results

The species area relationship for each plot was graphed with the universal curve predicted by METE, as well as with all other previous data (Figure 2). To determine if different

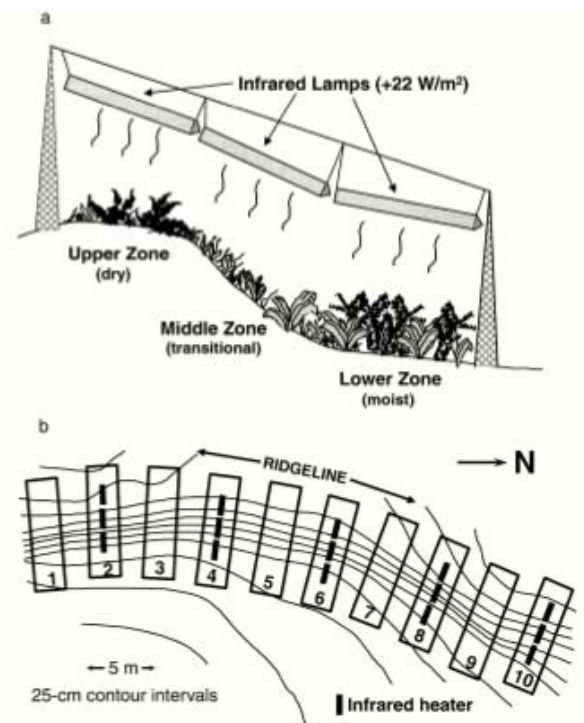


Figure 1. Warming meadow layout. Taken from Dunne, J.A. et al. 2004.

distances existed between the two treatments and the theoretical curve, distances were calculated from each point (representing slope against $\log(N/S)$) and a point on the curve. For the control plots, the mean distance of all three plots (1, 3, and 5) is 0.106. The relative deviation is 0.038. For the heated plots (2, 4, and 6), the mean distance is 0.044, with a relative deviation of 0.031. Contrary to our hypothesis, the control plots fall farther from the predicted curve than the warmed plots ($0.106 > 0.044$). Also calculated was the deviation of all previous data points from the theoretical curve, which is -0.032.

In concurrence with our calculated deviation, the highest frequencies were below zero (Figure 3). There was a significant difference from the “pooled”, or average plot data: for control plots, $p=0.006$ and for heated plots, $p=0.009$. The deviation for each individual plot was also graphed on the histogram (Figure 3). One control plot lies much below the theoretical curve (an even greater deviation than those of the previous data) but the other two plots are above the previous data deviations. Two of the control plots have deviations that lie above the theoretical curve, while one has a slight deviation below the curve (almost at zero).

The species abundance distributions were graphed for each plot (Figure 4). For all plots, both heated and controls, the observed abundances disagreed with the abundances predicted by METE, especially for species with low to intermediate abundances. Plots 1, 3, and 4 seem to have the least fitting observed abundances.

Discussion

The purpose of this experiment was to determine the validity of the Maximum Entropy Theory of Ecology in the control and heated plots of the Warming Meadow. We found that when looking at the species area relationship, both the heated and control plots tend to follow the universal scale-collapse curve predicted by METE. Though the tendency of the data from other previous undisturbed sites is to lie a little below the curve, the control plots in this study do not resemble this trend. Instead, both heated and control plot data tend to lie above the curve, but heated plot data is closer to the curve than the control plot data. Of all the plot data for both heated and control plots, only one control plot lies completely below the curve. When looking at the deviations of each individual plot, there is much variation within a small sample size, so little

can be concluded about the significance of the individual plot deviations when compared to the previous data series.

We found that for the species abundance distributions, all six plots barely follow a Fisher log series predicted by METE. The predicted and observed abundance distributions seem to disagree systematically with the theory for both control and heated plots, especially at low abundant species. So, contrary to our second hypothesis, the SADs did not differ between the control and heated plots. The deviation from observed and predicted abundance seems to even be greater in control plots than heated plots, as suggested by the graphed SADs (Figure 4). However, when looking at the values predicted by the theory for the abundance of the most abundant species, in most plots, the theory predicted correctly (Figure 5). In fact, two of the heated plots have very close observed values and METE predicted values. When looking at this study with past studies (Figure 6) the values fall nicely with previous data.

Conclusion

We believe there to be three possible conclusions as to why the theory predicted correctly for both heated and control plots. One suggestion this study makes is that the theory successfully predicts for undisturbed sites as well as disturbed sites. Another possible conclusion is that the heated plots are perhaps not disturbed enough for the theory to fail because not enough time has elapsed. From previous study conducted in the Warming Meadow, it is known that over time heating causes a shift in plant dominance (from forbs to shrubs), which changes the carbon cycling process. The plant community response to warming changed over time when faced with drought (drier soil) followed by change in species composition through a positive feedback system (Saleska et al. 2006). Perhaps over more time the changes in soil microclimate for example will increase enough for the theory to fail. On the other hand, responses to heating such as soil microclimate changes just described could be analyzed as the community acclimating to the heaters, which leads to our third possible conclusion that, again, the heated plots may not be disturbed from warming because they have adapted to 21 years of heating. The theory may have predicted correctly for the heated plots because the ecosystem may already be at a new equilibrium due to the gradual disturbance of heating. A greater “disturbance” could possibly have been observed after only five years of heating. Future studies in the RMBL

Warming Meadow may yield stronger conclusions to testing the Maximum Entropy Theory of Ecology with climate change.

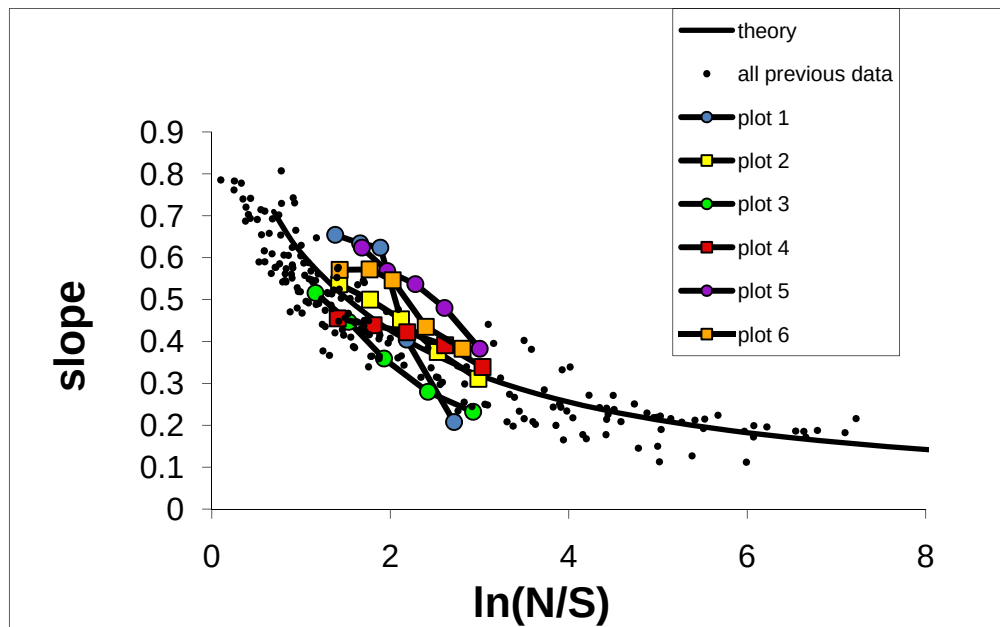


Figure 2. The species area curve including the theoretical curve predicted by METE, data from previous studies, and the warm and control plot data.

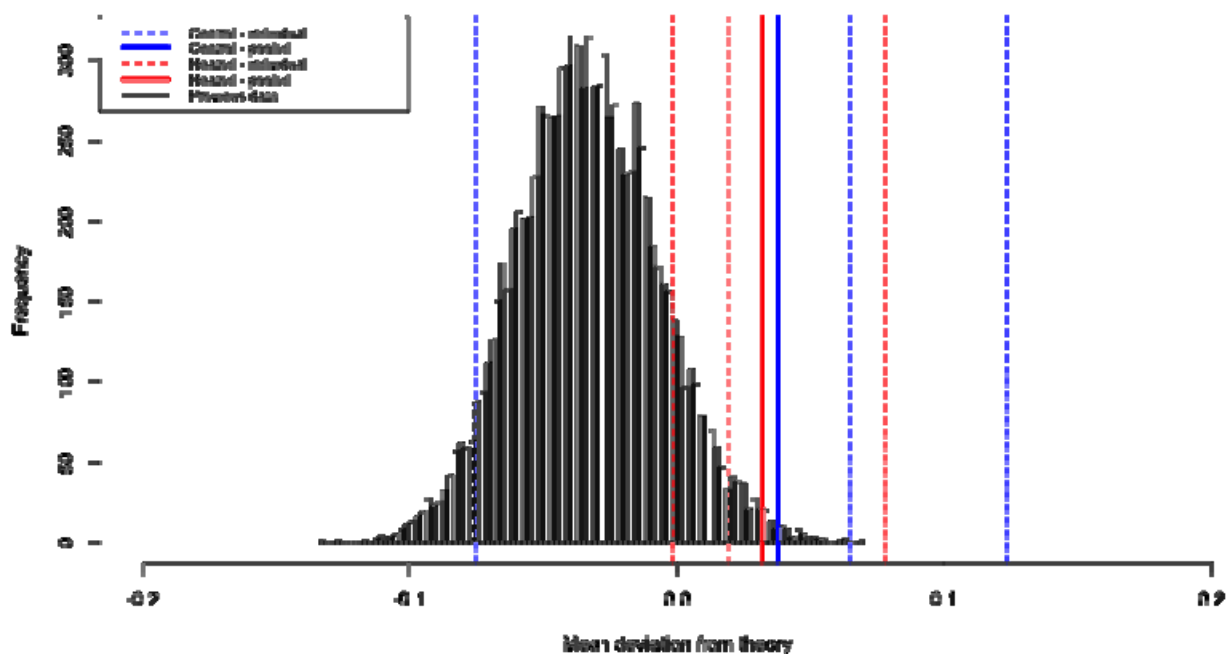


Figure 3. Histogram of the mean deviation of all previous data. Control plots mean relative deviation: 0.038 ($p < 0.01$), heated plots mean relative deviation: 0.031 ($p < 0.01$).

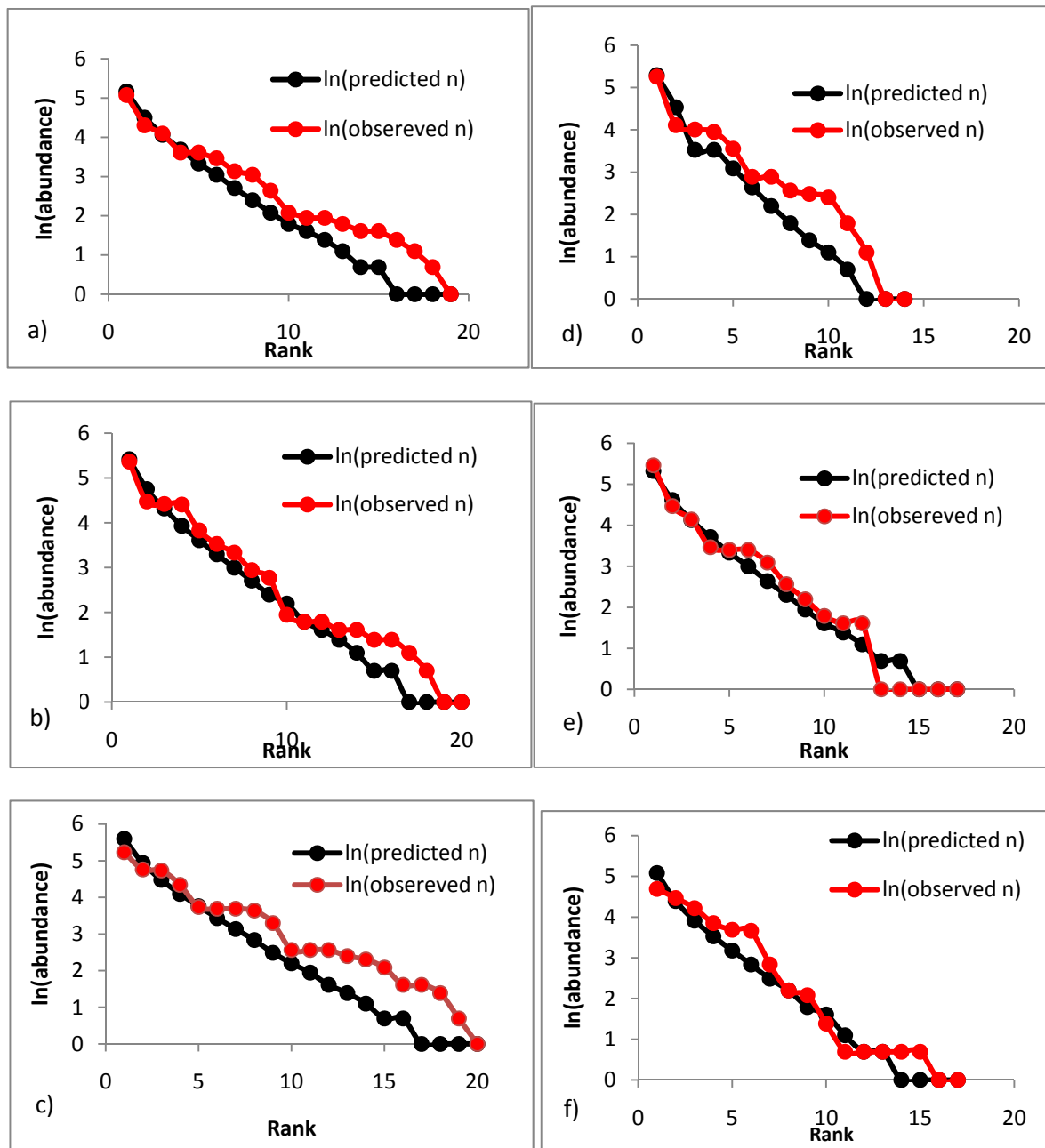


Figure 4. Observed and predicted species abundance distributions, Plots 1-6 (a-f).

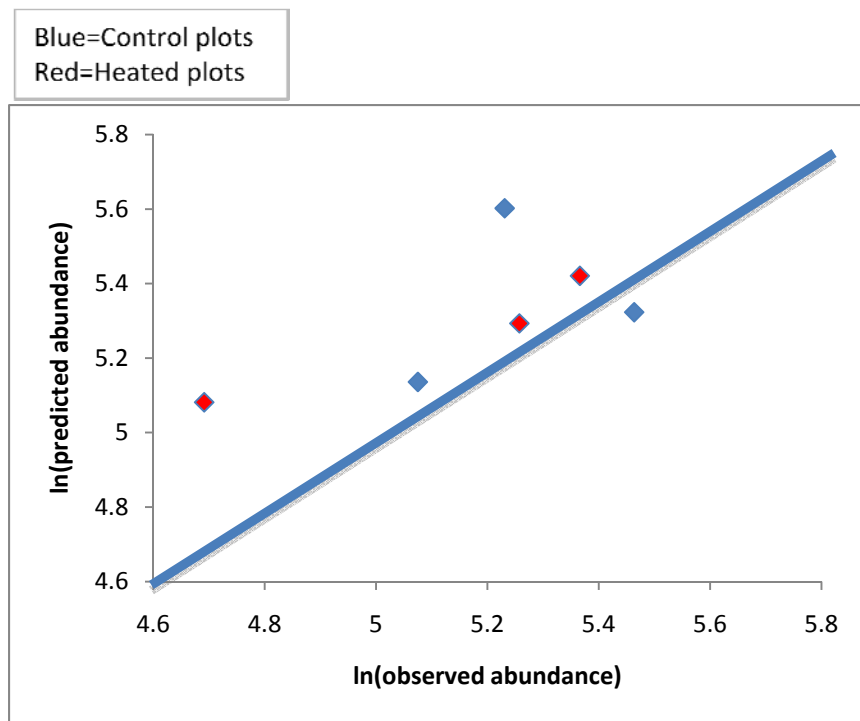


Figure 5. Abundance of most abundant species.

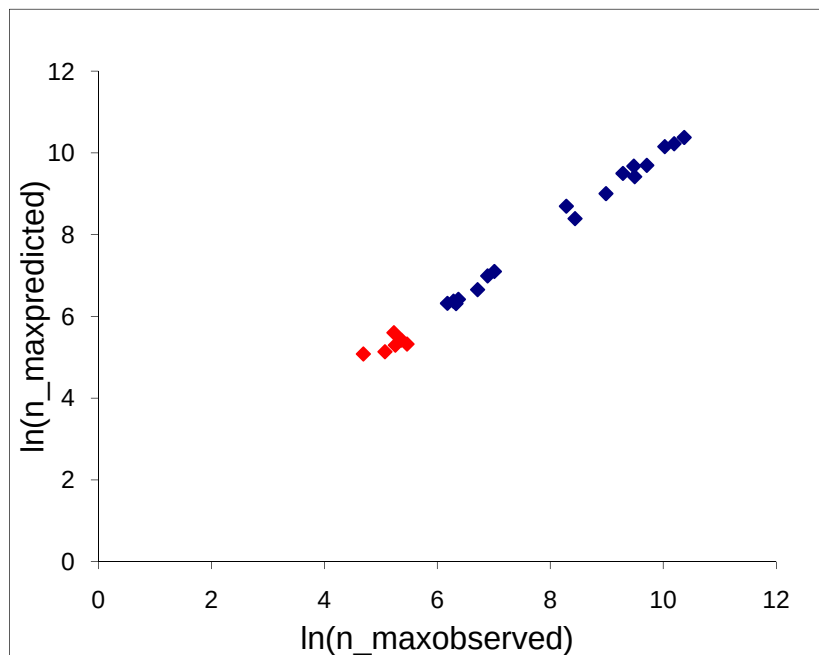


Figure 6. Abundance of most abundant species. Red points are the six plots from this study, while the blue points are from previous studies.

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