



Testing the predictions of the Maximum Information Entropy Theory for abundance and energy distributions on the Gothic earthflow

Student: Arianne F. Messerman

Mentors: Dr. John Harte and Erica Newman, M.S.

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Abstract

Maximum Information Entropy theory, or MaxEnt, has been shown in many cases to accurately predict relationships between macroecological variables in ecosystems in a state of equilibrium. However, little testing has been performed on MaxEnt in disturbed sites. This study evaluated the accuracy of predictions made by MaxEnt for metabolic rate distributions among and across plant species on a high-disturbance earthflow in Gothic, Colorado. My results showed that the quality of MaxEnt predictions of metabolic rate distributions varied between metric examined, as well as plot and species observed. In disagreement with previous studies, abundance distributions were accurately predicted across all stages of succession for which measurements were taken. The findings of this study may prove to be of interest to disturbance ecologists and conservation efforts in general.

Keywords

Disturbance Ecology, Succession, Metabolic Rate, Maximum Information Entropy Theory, MaxEnt, Earthflow

Total ecosystem area, total number of individuals in a community, species richness, and total metabolic energy rate are important variables in environments of all types and at every scale. The ability to accurately determine ecological relationships that are dictated by these variables is critical for understanding the structure and function of ecosystems. Additionally, being able to calculate values for such relationships in any ecosystem can ease the process of taking a census at any given site, allow researchers to predict abundance and diversity data from an incomplete census, predict extinction rates due to habitat loss, as well as determine which interactions have the greatest effects on a particular ecosystem (Harte *et al.*, 2008).

Macroecological patterns can be mathematically defined by metrics and are often assumed to be described by power law functions. However, these power laws have frequently been shown to lack universality when a large variety of ecosystems, species and scale ranges have been studied (Preston 1962; May 1975; Plotkin *et al.*, 2000 a, b; Green *et al.*, 2002; He & Legendre 2002; and Drakare *et al.*, 2006). A new theory was recently proposed to better predict these macroecological trends. Maximum Information Entropy (MaxEnt) theory has proven reliable for providing reasonable estimations of the species-area relationship (SAR), endemic-area relationship (EAR), the species-abundance distribution (SAD), and the distribution of metabolic rates across individuals and across species within a defined study area (Harte *et al.*, 2008).

Previous testing of MaxEnt has been performed primarily on ecosystems in or near a state of equilibrium (Harte *et al.*, 2008). However, some evidence suggests that predictions made by MaxEnt for sites undergoing a middle successional period may be less accurate due to the occurrence of rapid diversification at that time (Harte & Gruner, unpublished). For example, the



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Fisher log-series curve. However, one study performed on plant species on an earthflow in Gothic, Colorado found that the observed trend was best described by a log-normal distribution (Newman & Harte, unpublished; Bartholomew 2009). These results are similar to findings from work done on moths in the United Kingdom (Kempton & Taylor 1974) and Hawaiian arthropods as well (Harte & Gruner, unpublished).

In this study, I compared the theoretical predictions made by MaxEnt for metabolic rate distributions among individuals, and between species across various successional stages at the Gothic earthflow, to measured values from those sites. Based on the above-mentioned inaccuracy seen in predictions made by MaxEnt for disturbed sites thus far, I hypothesized that MaxEnt theory would not accurately predict distributions of metabolic rate at all successional stages on the earthflow, as this site is far from equilibrium. The results of this study may be of value to conservationists attempting to understand and restore areas disturbed by humans or natural processes.

Methods

The earthflow used as a study site in this experiment was formed in the spring of 1923. It is located 5 km south of the Rocky Mountain Biological Laboratory in Gothic, Colorado (11° 13' 86"). (Curtin 1994). Researchers believe that water seepage from an irrigation ditch lead to the destabilization of the sediment in the slide portion of the hill (Curtin 1994). The upper third of the hill then slumped as the remainder slid, allowing some of the original vegetation from the top of the hill to remain intact as the event took place (Langenheim 1949, 1956). In contrast, the segment of the hill that slid became a severely disturbed area approximately 1 km wide and 2 km long (Langenheim 1949, 1956). The result of this event was a west-facing slope standing from

about 3,300 m (Curtin 1994). Today, the vegetative composition of the undisturbed surrounding areas remains different than that of the earthflow.

This is one indication that the site is still undergoing succession.

To examine the accuracy of predictions made by MaxEnt over a successional gradient at this site, my mentor Erica Newman and I selected three plots on the highly disturbed, relatively flat portion of the earthflow. Each site was chosen based on a visual estimation of vegetative cover as an indicator of successional stage. We placed plot A on the far south end of the earthflow in an area with approximately 10% vegetative cover. Plots B and C were located to the north of plot A in order across the earthflow, with approximately 50% and 30% vegetative cover, respectively. Each of the three disturbance plots were placed within Newman's larger SAR study sites, which were themselves selected to have comparable slope, aspect, and elevation. These similar characteristics insured that any differences between the MaxEnt predictions and observed values of abundance and metabolic rate could be attributed to the earthflow disturbance, and not to other local conditions. Additionally, we established one control plot (plot D) outside of the earthflow. Aspen forests that bracketed our study site had a largely different vegetative community than the disturbed area. For this reason, we placed the control plot on top of the earthflow, again within one of Newman's MaxEnt SAR study plots. We took care to avoid establishing the control plot in an area with abundant invasive species. This experimental design better allowed us to interpret succession following the earthflow event, without having to take into account the disturbance caused by invasion (Newman & Harte, personal communication).

We then designated the four $4 \times 4 \text{ m}^2$ plots using nails and string. To ensure that each plot was a perfect square, we cut two sections of string that were $4\sqrt{2} \text{ m}$ long each. We then

equally taut across the diagonals of the plot. To ease the task of plant counting, we set up a grid system of string that divided the plots into $1 \times 1 \text{ m}^2$ cells. I was then able to collect GPS coordinates for the corners of each plot using a 2005 series GeoXT mapping unit (Trimble, Centennial, CO).

We began data collection by identifying all forbs, shrubs, and native bunch grasses within each plot. As we did so, we also recorded the abundance of each species. To determine total metabolic rate and metabolic rate for each individual and species, I used the previous allometric finding that total leaf area (A) scales as body mass (M) to the $3/4$ power ($A \propto M^{3/4}$) (Niklas & Enquist, 2001). Metabolic scaling theory states that $B \propto M^{3/4}$, where B is metabolic rate (Niklas & Enquist, 2001). It could then be said that $A \propto B$. Thus, total leaf area served as a proxy measure of metabolic rate.

I found total leaf area by first sampling leaves from each individual of a species and estimating the mean leaf area of these samples soon after abundance data had been collected. I sampled average sized-leaves from those species with more uniform leaves, and sampled over the range of available leaf sizes for those species that displayed greater variability in single leaf area. The number of leaves I chose to sample for each species depended upon the size of the individual, as well as the number of leaves common to the species. After leaves had been collected and pressed, I scanned all leaf samples and found leaf area using the computer program ImageJ (Rasband 1997-2009). Average leaf area was then estimated for each individual, as well as each species.

I proceeded by counting the leaves on all individuals within each plot. I determined leaf number exactly for small plants and species with few leaves. For a larger individual or species with more abundant leaves, I estimated the leaf count by approximating the number of leaves on

ing all of the branches on the individual. Multiplying leaf counts by mean leaf area allowed me to calculate total leaf area for individuals and species within a single plot. Due to some confusion about which leaf samples corresponded to each individual, I found plot C total leaf areas by using the average leaf area of all members of each species multiplied by specific individual leaf counts. I then used total leaf area values to estimate metabolic rate using the above formula.

Once abundance data and metabolic rate values had been obtained, I analyzed the distributions of metabolic rates between and across species by graphing the observed data in rank-variable format. MaxEnt metabolic rate distribution predictions were then calculated using the following equations all taken from Harte *et al.* (2008):

- The distribution of metabolic rate across the individuals in a single species of abundance n ($\Theta(\varepsilon|n)$) was predicted for species with abundances of five or more from the equation

$$\Theta(\varepsilon|n, S_0, N_0, E_0) \approx \lambda_2 n e^{-\lambda_2 n (\varepsilon-1)}$$

where N_0 is the total number of individuals, S_0 is the total number of species, E_0 is the total metabolic rate of all individuals, λ_2 is the Lagrange multiplier given by S_0/E_0 , and ε is the metabolic rate of an individual (Harte *et al.*, 2008; Harte *et al.*, 2009). The units of ε and E_0 are normalized such that the individual with the lowest metabolic rate has $\varepsilon=1$.

- The distribution of metabolic rates averaged over all individuals within a species ($\nu(\bar{\varepsilon})$) was predicted from the equation

$$\nu(\bar{\varepsilon}|n, S_0, N_0, E_0) \approx \frac{1}{\ln(\frac{1}{\beta})} \cdot \frac{e^{\frac{-\beta}{\lambda_2(\bar{\varepsilon}-1)}}}{(\bar{\varepsilon}-1)}$$

where β satisfies the equation $\beta \ln(1/\beta) = S_0/N_0$ and $\bar{\varepsilon}$ is average metabolic rate of the individuals in a species (Harte *et al.*, 2008; Harte *et al.*, 2009).

for all individuals in a community ($\Psi(\varepsilon)$) was predicted from the equation

$$\Psi(\varepsilon | n, S_0, N_0, E_0) \approx \lambda_2 \cdot \beta \cdot \frac{e^{-\gamma}}{(1 - e^{-\gamma})^2}$$

where and $\gamma = \alpha_1 + \alpha_2 \bar{U}$ (Harte *et al.*, 2008; Harte *et al.*, 2009).

The rank-metabolism relationship for the distributions of $\Theta(\varepsilon | n)$ and $\Psi(\varepsilon)$ are given by the following equations, respectively:

$$\varepsilon_\theta(r, n) = 1 + \frac{1}{(\lambda_2 n)} \cdot \ln \left(\frac{n}{(r - \frac{1}{2})} \right)$$

$$\varepsilon_\psi(r) = \frac{1}{\lambda_2} \cdot \ln \left(\frac{\beta N_0 + r - \frac{1}{2}}{r - \frac{1}{2}} \right) - \frac{\lambda_1}{\lambda_2}$$

where r is rank and $\alpha_1 = \beta - \alpha_2$ (Harte *et al.*, 2008; Harte *et al.*, 2009). Outputs from these formulas and the above function for $v(\bar{\varepsilon})$ were compared to the measured rank-metabolism data to determine the quality of MaxEnt predictions in the disturbed site.

Similarly, the distribution of abundances across species ($\Phi(n | S_0, N_0)$) is predicted to be the fisher log-series distribution

$$\Phi(n | S_0, N_0) \approx \frac{1}{\ln(\frac{1}{\beta})} \cdot \frac{e^{-\beta n}}{n}$$

Again, the measured data was compared to MaxEnt predicted abundances on rank-abundance graphs to analyze the accuracy of predictions made by MaxEnt. When graphing abundance and metabolic rate predicted values against measured ones, a near one-to-one relationship between the two variables and a high R^2 value were indicative of high accuracy in the predictions made

MaxEnt prediction accuracy between sites of varying successional stages were assessed.

Next, I analyzed how well my data supported energy equivalence, the idea that all species utilize equal shares of the total available energy. In other words, energy equivalence implies that individuals in more abundant species will have lower metabolic rates than less abundant species. Due to the above-mentioned observation that $B \propto M^{3/4}$, I anticipated that a graph of species abundance for each plot against average mass per species would yield a slope of -3/4 if energy equivalence was supported.

Results

MaxEnt predictions for the average metabolic energy rates for each species ($\bar{\epsilon}$) showed poor accuracy across the 3 measurement plots (Figures 1 and 2). In all plots, the species with the lowest average metabolic rates were over-predicted by MaxEnt, while the species with the highest average metabolic rates were under-predicted by MaxEnt. The model best fit the collected data for plot B with a slope of 0.27 and an R^2 value of 0.59. Slopes of 0.16 and 0.08 were found in comparing predicted and measured average metabolic rate values for plots A and C. Plot D also showed poor agreement between the predicted and observed $\bar{\epsilon}$ values with a slope of 0.26 and an R^2 value of 0.62.

Distributions of metabolic rates across all individuals in a community ($\Psi(\epsilon)$) were well predicted by MaxEnt for all measurement plots, but not for plot D (Figures 3 and 4). Of the measurement plots, plot B metabolic rate data resulted in the slope farthest from a one to one relationship between predicted and measured metabolic rates with a value of 1.52. The R^2 value for this plot was also the lowest at 0.72. These values may be attributed to outliers amongst the

ates. Excluding the 10 largest data points (which have the highest leaf number estimation errors) from analysis revealed a closer relationship between MaxEnt predictions and the measurements. In contrast to plots A, B and C, plot D ϵ values were poorly predicted by MaxEnt with a slope of 0.31.

The accuracy of predicted metabolic rates across the individuals in a single species of abundance n ($\Theta(\epsilon|n)$) made by MaxEnt was the least variable for the three most abundant species in plot A (Figures 5 and 6). The second and third species, *Eriogonum umbellatum* and *Ericameria nauseosus* (formerly *Chrysothamnus nauseosus*), were only slightly over-predicted by MaxEnt with slopes of 1.20 and 1.59, respectively. The most abundant species in plot A was *Heterotheca villosa*. This species was under predicted by MaxEnt (as it was in every plot) with a slope of 0.10. All 3 species had high R^2 values describing the relationship between predicted and measured metabolic rates.

Plot B showed little accuracy in the predictions made by MaxEnt for $\Theta(\epsilon|n)$ (Figures 7 and 8). *H. villosa* and *Vicia americana* were the two most abundant species in this plot. Neither species was predicted well by MaxEnt with slopes of 0.09 and 3.70, respectively. Predictions became more accurate for species of intermediate abundance such as *E. umbellatum*, *E. nauseosus* and *Artemisia tridentata*. For each of these species $\Theta(\epsilon|n)$ remained slightly under-predicted or over-predicted. The four species that were analyzed for $\Theta(\epsilon|n)$ with the lowest abundances (*Ipomopsis aggregata*, *Erigeron speciosus*, *Viola nuttallii* and *Mertensia fusiformis*) again showed a decline in the quality of MaxEnt predictions with predicted ϵ values being consistently higher than measured data. Despite the inaccuracy of MaxEnt predictions for $\Theta(\epsilon|n)$ in plot B, no species showed an R^2 value lower than 0.86.

variation in the accuracy of predictions made for $\Theta(\varepsilon|n)$ in plot C as was seen in plot B (Figures 9 and 10). The 3 most abundant species in this plot were *H. villosa*, *Achillea millefolium* and *V. nuttallii*. Again, metabolic rates were highly over-predicted or under-predicted for all 3 of these species by MaxEnt theory. Less abundant species such as *E. speciosus*, *E. umbellatum* and *A. tridentata* were more closely predicted by MaxEnt theory with slopes of 1.82, 1.00, and 1.16. However, the least abundant species in plot C (*I. aggregata* and *Taraxacum officinale*) again showed substantially lower metabolic rate distributions than those predicted by MaxEnt. In this plot, no R^2 value dropped lower than 0.74.

MaxEnt predictions of the $\Theta(\varepsilon|n)$ distributions for plot D generally became less accurate with declining species abundance (Figures 11 and 12). The most abundant species in this plot, *A. millefolium*, revealed a slope of 10.85 when predicted ε values were compared to measured ones. In contrast, *Agoseris glauca* was the least abundant species in plot D, and had a slope of 30.28. Again, R^2 values were no lower than 0.85 for these species.

The distribution of abundances across species ($\Phi(n|S_0, N_0)$) was predicted accurately by MaxEnt for all 4 plots (Figures 13 and 14). Plot C had the slope closest to 1.00 at 0.95, while plot D had the slope furthest from 1.00 at 0.84. Plots A and B had intermediate slopes of 0.86 and 0.88, respectively. Variability was low with no R^2 value dropping below 0.98.

A comparison of abundance over average mass for each plot yielded no consistent trend (Figure 15). Slope was highly variable between plots and there was a great degree of scatter.

Discussion

The aim of this study was to investigate the accuracy of MaxEnt theory in predicting metabolic rate and abundance distributions across a successional gradient. My data supported the

ns are not reliable over all successional stages on the disturbed site.

Predicted values of $v(\bar{\epsilon})$, the distribution of metabolic rates averaged over all individuals in a species, were inaccurate for all four plots observed. Of the measurement plots, plot B was slightly better predicted than plot A, and predictions for plot A were a little more accurate than those for plot C. MaxEnt's failure to accurately predict $v(\bar{\epsilon})$ distributions may be attributed to the disturbed nature of the site. Additionally, poor predictions may have been due to inadequate methods for extrapolating metabolic rate data for a particular species. For example, it may have been that total leaf area was, by itself, not an adequate proxy for metabolic rate due to plant structure.

Of all the energy metrics examined, $\Psi(\epsilon)$ metabolic rate distributions were the most accurately predicted for the 3 measurement plots. In this portion of the study, plot C was better predicted than plot A. Plot B had the least accurate predictions and greatest amount of variability amongst quality of projections made for individuals with high leaf area. In fact, examining this metric without the 10 individuals with the highest leaf areas produced a much better fit between measured and predicted data. In contrast, species with lower metabolic rates were predicted more accurately for plot B than for plot C. This indicated that the performance of MaxEnt varied between metabolic rate values, as well as plot and metric observed.

$\Theta(\epsilon|n)$, the distribution of metabolic rates across all individuals of a species of abundance n , displayed MaxEnt predictions that were the most accurate for plot A. At this site, the only species that was extremely under-predicted was *H. villosa*. Further analysis showed that *H. villosa* was under-predicted (and more extremely so) in the other 2 measurement plots as well. This species-dependent trend may indicate that total leaf area was not a good predictor of

ing 2 species were both slightly under-predicted by theory, but not to an outstanding degree.

Plots B and C showed similar trends when measured and predicted $\Theta(\varepsilon|n)$ distributions were investigated. In both plots, the most abundant species were poorly predicted, the middle abundant species were best predicted, and the least abundant species were highly over-predicted by MaxEnt. Inaccurate predictions may have been due to reduced performance by the model due to disturbance. It is possible that the same trend was not seen in plot A due to the lower number of species present with more than five individuals. Reexamining this metric with the use of larger plots (and thus an increased number of individuals) may shed light on this point in future studies. Interestingly, despite the degree of inaccuracy of predictions made, R^2 values remained incredibly high for all tests of $\Theta(\varepsilon|n)$. This might be due to inaccuracies in the method of using total leaf area as a surrogate for metabolic rate. If metabolic rate values were consistently incorrect by multiplicative factors due to different physiologies specific to each species, then the above findings of low accuracy in predictions made by MaxEnt with the same distribution shape as the measured values might be explained. The question then becomes why $\Psi(\varepsilon)$ predictions were so accurate. This query demands further investigation.

For all of the above metabolic rate metrics examined, MaxEnt performed poorly in making predictions for the control plot (plot D). Predictions made for this plot over or under-predicted metabolic rate values often to a higher degree than did the predictions made for the measurement plots. This unexpected result is likely due to the fact that plot D was disturbed. As the study period progressed, it became evident that cattle grazed the top of the earthflow more frequently than I had originally thought. Disturbance due to herbivory may be the reason that

Other sites in equilibrium were not observed in the control plot for this study (Harte *et al.*, 2000; Harte *et al.*, 2009).

The distribution of abundance across species ($\Phi(n|S_0, N_0)$) was very well predicted by MaxEnt for all 4 plots. This was surprising, as previous studies have shown that species abundance distributions are not accurately predicted in disturbed sites, including the Gothic earthflow (Kempton & Taylor 1974; Bartholomew 2009; Harte & Gruner, unpublished). $\Phi(n|S_0, N_0)$ distributions are predicted by MaxEnt to be the Fisher log-series distribution, but highly disturbed ecosystems produce log-normal curves (Kempton & Taylor 1974; Bartholomew 2009; Harte & Gruner, unpublished; Newman & Harte, personal communication). However, in this study the only plots to show slight log-normal behavior were plots C and D. Results from Newman's current SAR study using 16x16 m² plots on the Gothic earthflow should allow me to better interpret these findings in the near future.

A final point of interest in this study was that there was no apparent relationship between abundance and average mass of a species for any of the plots. Energy equivalence would produce a slope of -3/4 on a log-log graph of mass versus abundance. If total leaf area was an adequate surrogate for metabolic rate, then these data fail to support energy equivalence. However, the variation seen in these data could be attributed to poor estimates of ϵ if total leaf area was not a good proxy for metabolic rate. In this case, the analysis of the above metabolic rate metrics will need to be performed using a different method to determine energy distributions. Again, the accuracy seen in the predictions made for $\Psi(\epsilon)$ should be evaluated.

MaxEnt theory has been shown to work very well for predicting metabolic rate and abundance distributions in undisturbed ecosystems (Harte *et al.*, 2008). However, this study has shown that the model makes less accurate projections for metabolic rate distributions on the

These results, future studies should consider using a different method to more accurately measure metabolic rates for all species. This might be accomplished by using photosynthetic rate values as a proxy for metabolic rate (Benjamin Blonder, personal communication). Larger plots and the addition of replicate plots would provide larger sample sizes and expose any plot-specific conditions that could affect our results unrelated to successional stage. To determine whether MaxEnt makes stronger projections for communities undergoing an earlier successional stage than those experiencing later successional stages, gaining additional insight into the rates of change occurring in the plots will be necessary. Examining data from previous studies performed on the Gothic earthflow may enable us to conduct this analysis.

It is of great importance that the subject of MaxEnt prediction quality across successional stages continues to be studied in a variety of different disturbed areas. Such investigations will provide us with new insight into the commonality or rarity of patterns observed on the Gothic earthflow. Creating a more solid understanding of these trends will allow us to adapt MaxEnt theory to better predict the energetics of disturbed sites. This knowledge will likely be valuable for future studies in disturbance ecology and restoration efforts.

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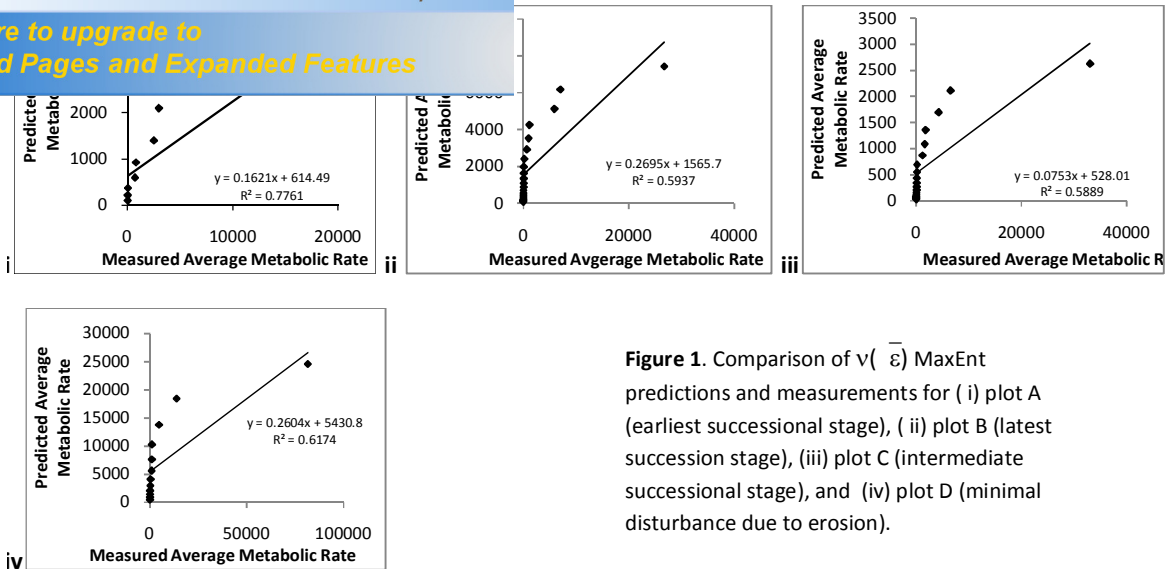


Figure 1. Comparison of $v(\bar{\epsilon})$ MaxEnt predictions and measurements for (i) plot A (earliest successional stage), (ii) plot B (latest succession stage), (iii) plot C (intermediate successional stage), and (iv) plot D (minimal disturbance due to erosion).

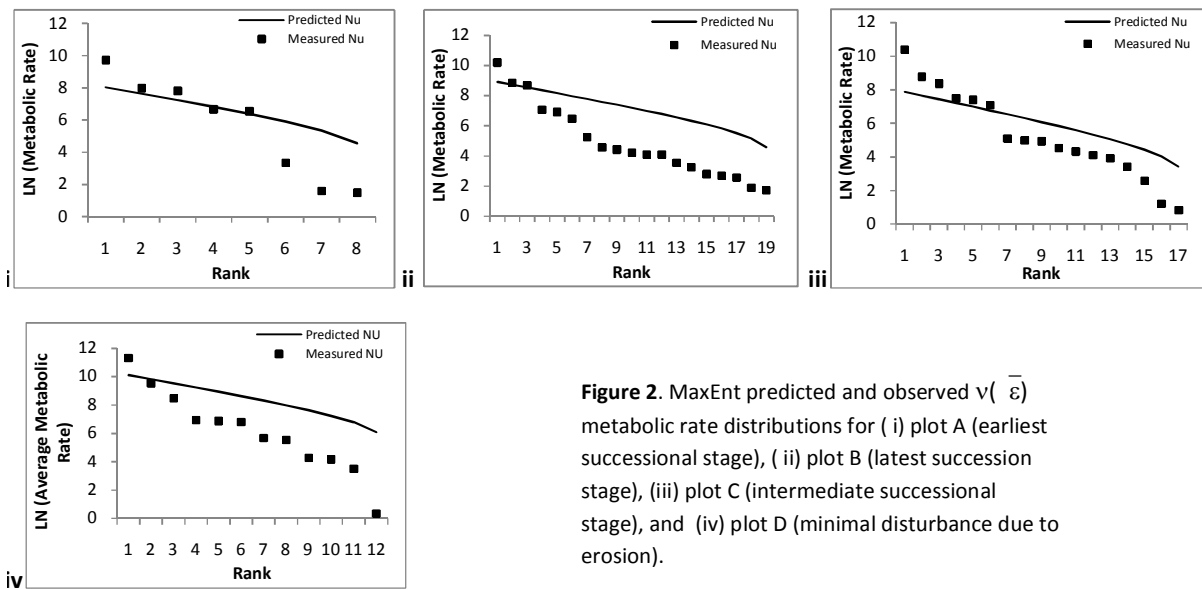
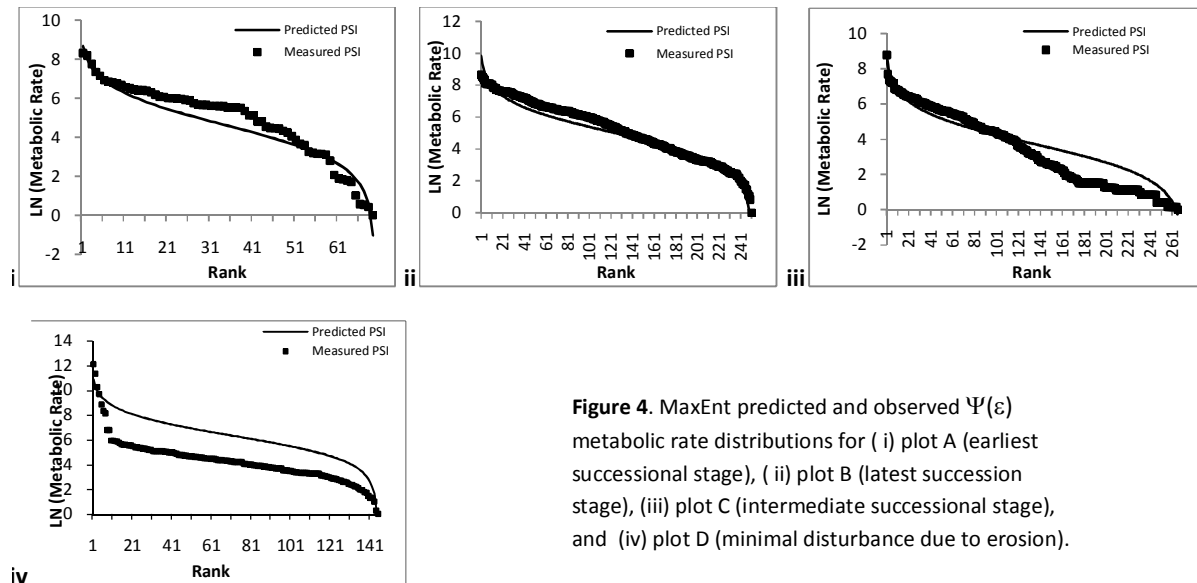
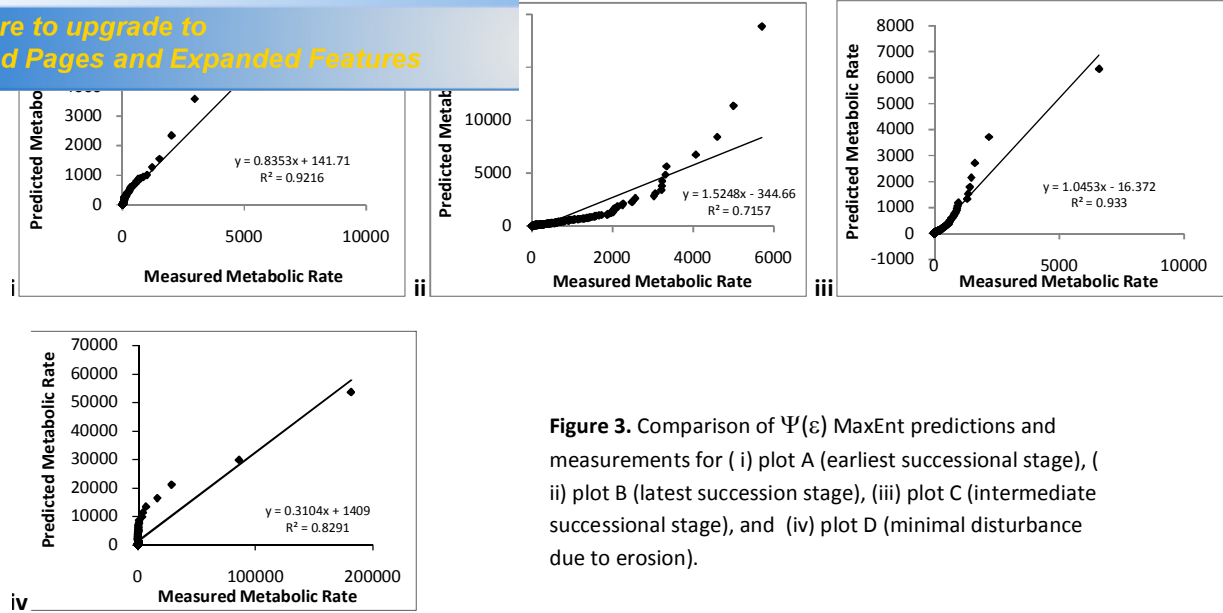


Figure 2. MaxEnt predicted and observed $v(\bar{\epsilon})$ metabolic rate distributions for (i) plot A (earliest successional stage), (ii) plot B (latest succession stage), (iii) plot C (intermediate successional stage), and (iv) plot D (minimal disturbance due to erosion).



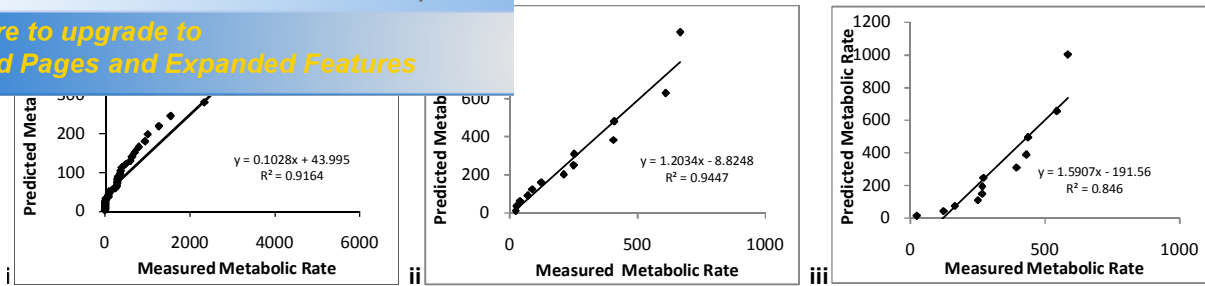


Figure 5. Comparisons of $\Theta(\varepsilon|n)$ MaxEnt predictions and measurements for the three most abundant species (i-iii are species 1-3) in plot A (earliest successional stage).

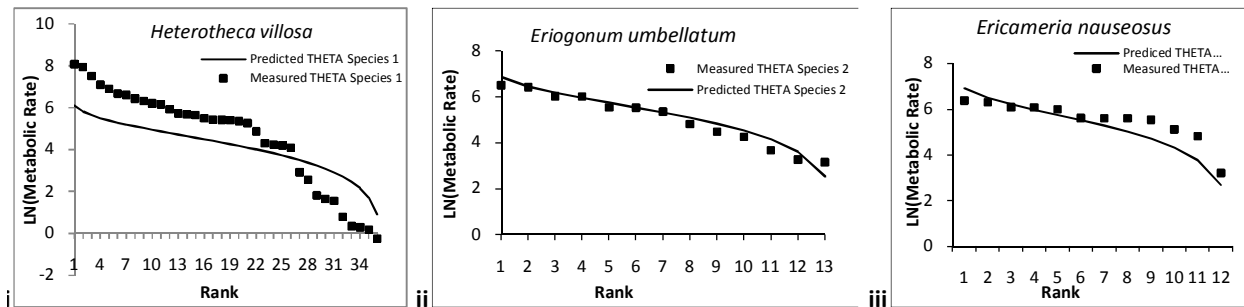


Figure 6. MaxEnt predicted and observed $\Theta(\varepsilon|n)$ metabolic rate distributions for the three most abundant species (i-iii are species 1-3) in plot A (earliest successional stage).

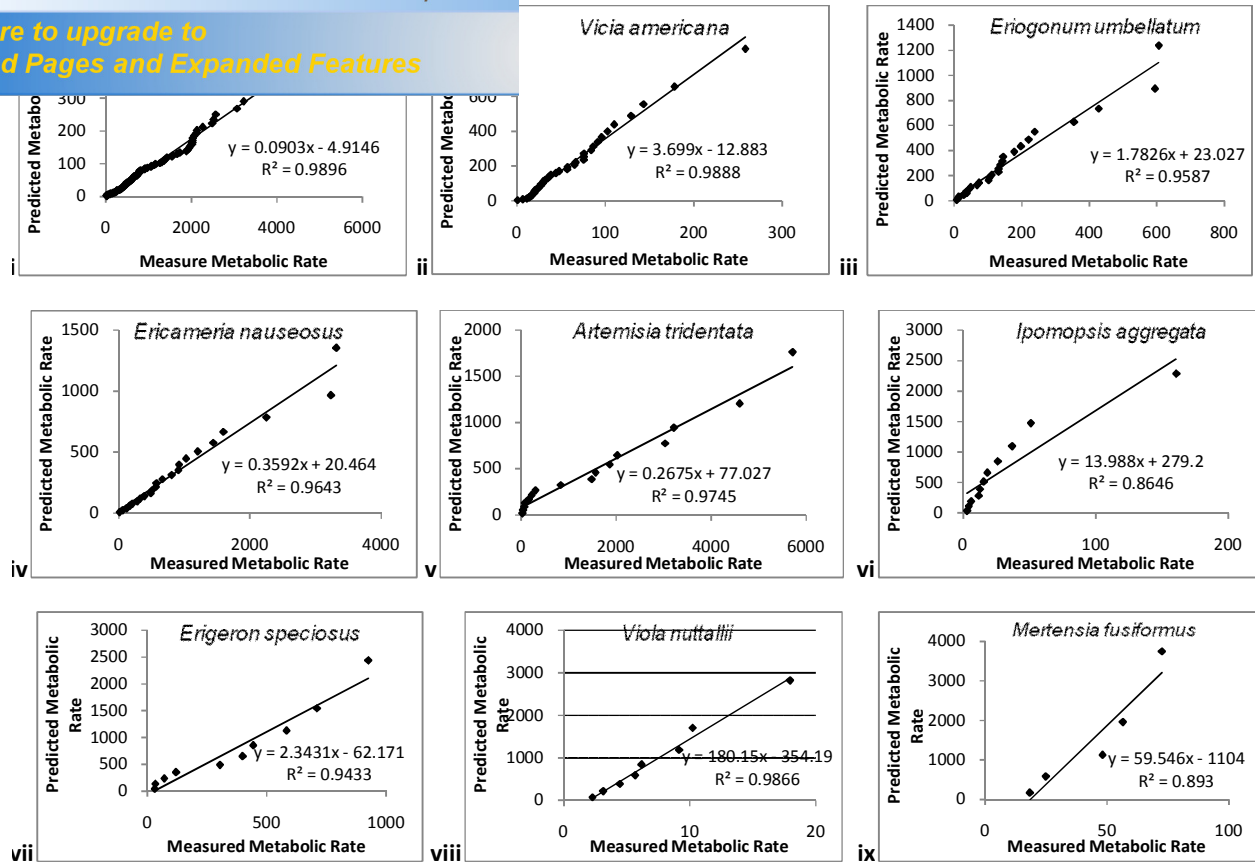


Figure 7. Comparisons of $\Theta(\varepsilon|n)$ MaxEnt predictions and measurements for the nine most abundant species (i-ix are species 1-9) in plot B (latest successional stage).

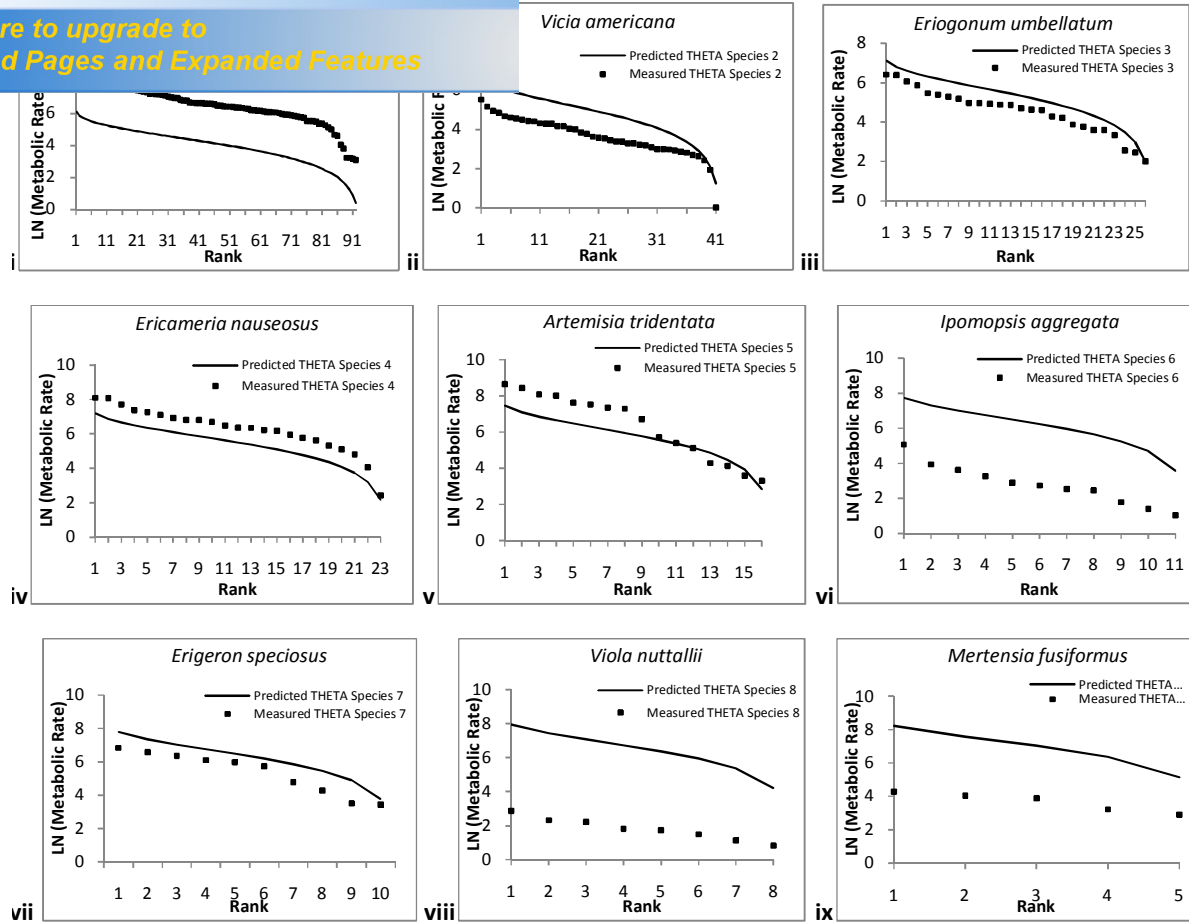


Figure 8. MaxEnt predicted and observed $\Theta(\varepsilon|n)$ metabolic rate distributions for the nine most abundant species (i-ix are species 1-9) species in plot B (latest successional stage).

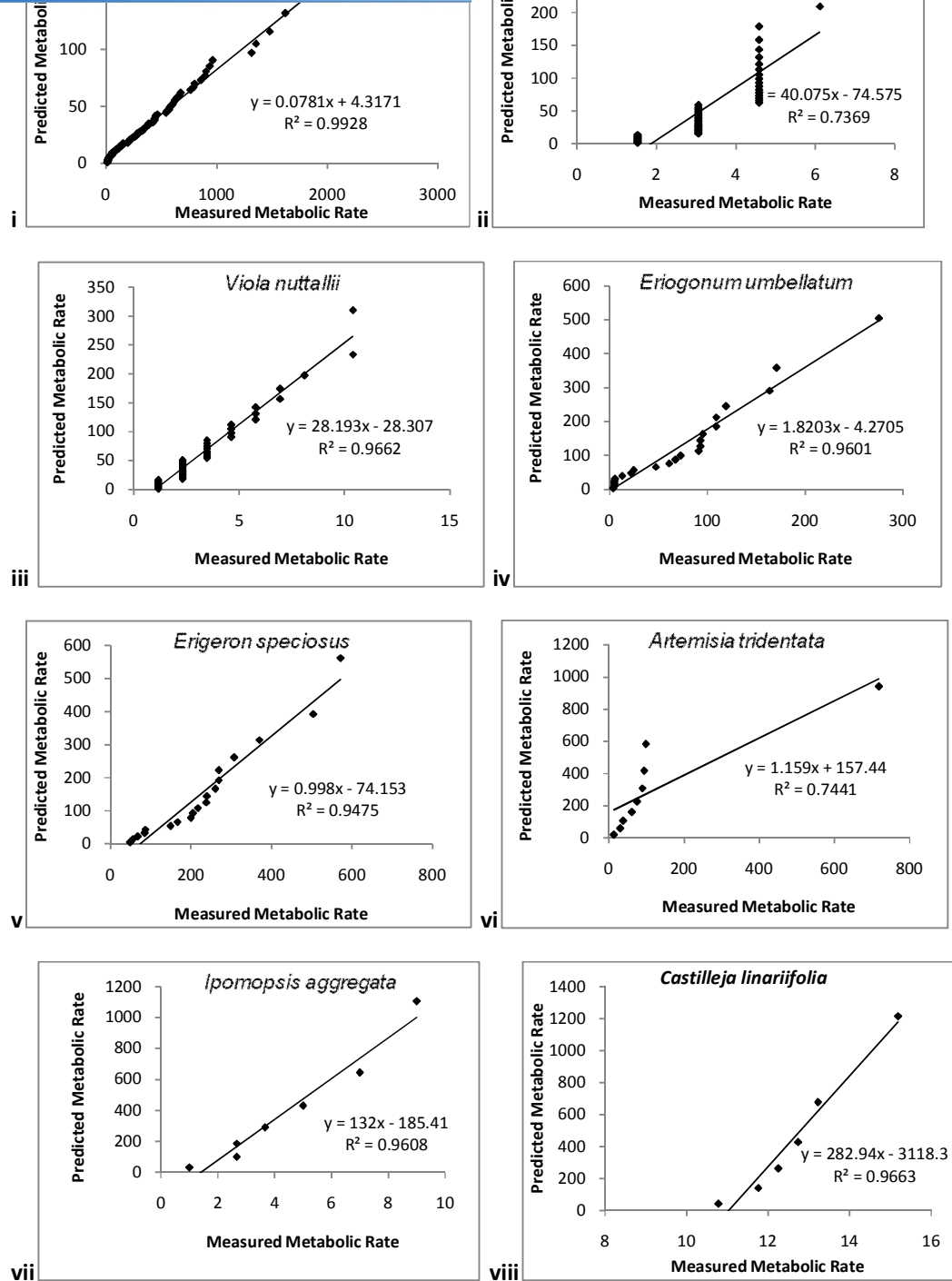


Figure 9. Comparisons of $\Theta(\varepsilon|n)$ MaxEnt predictions and measurements for the eight most abundant species (i-viii are species 1-8) in plot C (intermediate successional stage). See text for differences in measuring methods compared to other plots.

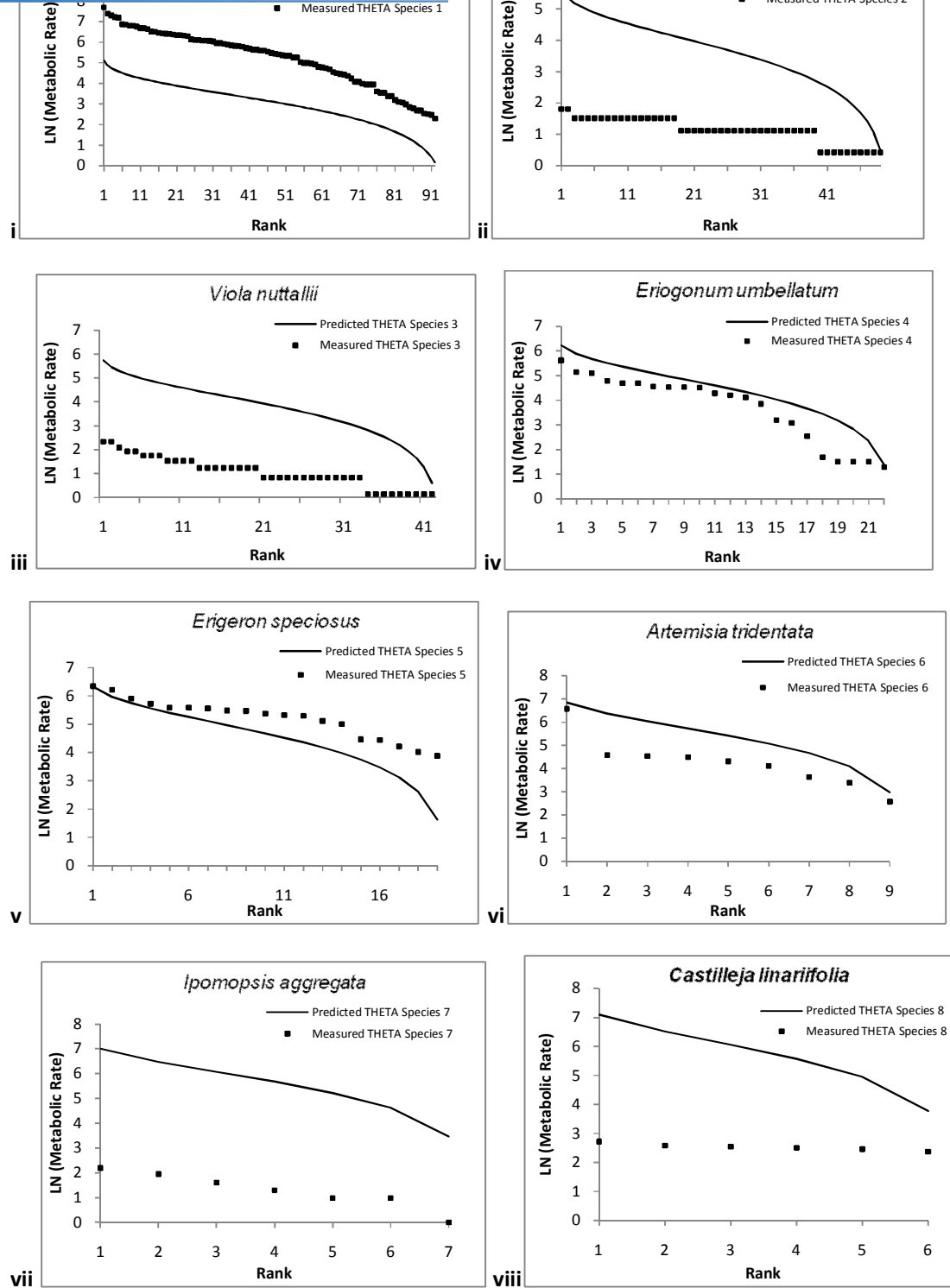


Figure 10. MaxEnt predicted and observed $\Theta(\epsilon|n)$ metabolic rate distributions for the eight most abundant species (i-viii are species 1-8) in plot C (intermediate successional stage).

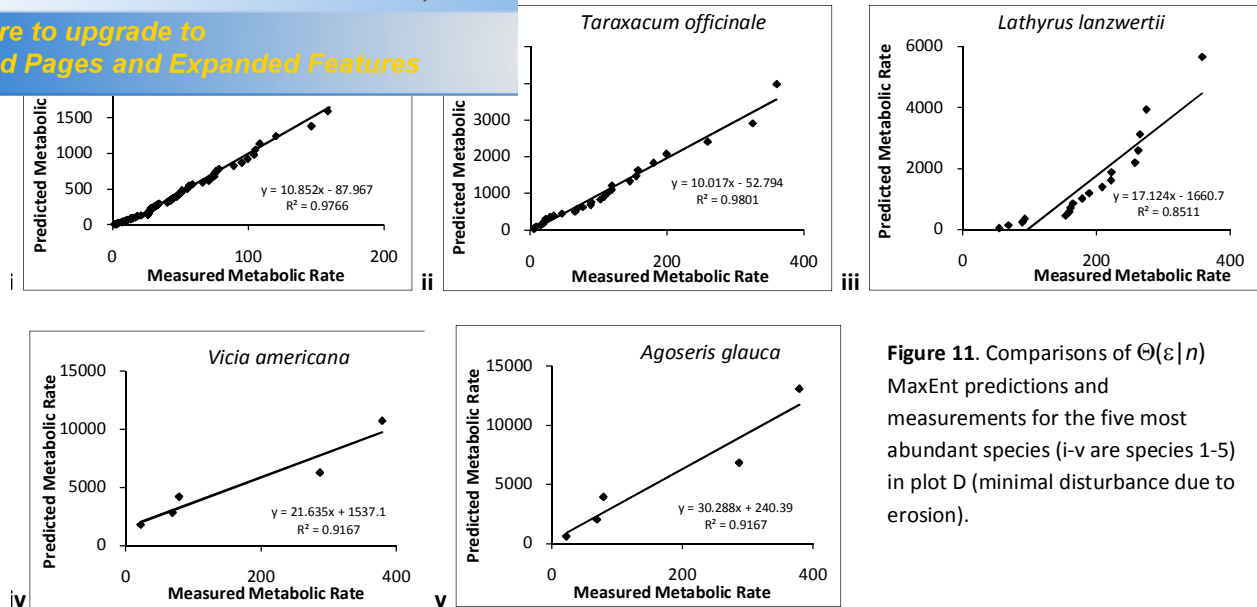


Figure 11. Comparisons of $\Theta(\varepsilon|n)$ MaxEnt predictions and measurements for the five most abundant species (i-v are species 1-5) in plot D (minimal disturbance due to erosion).

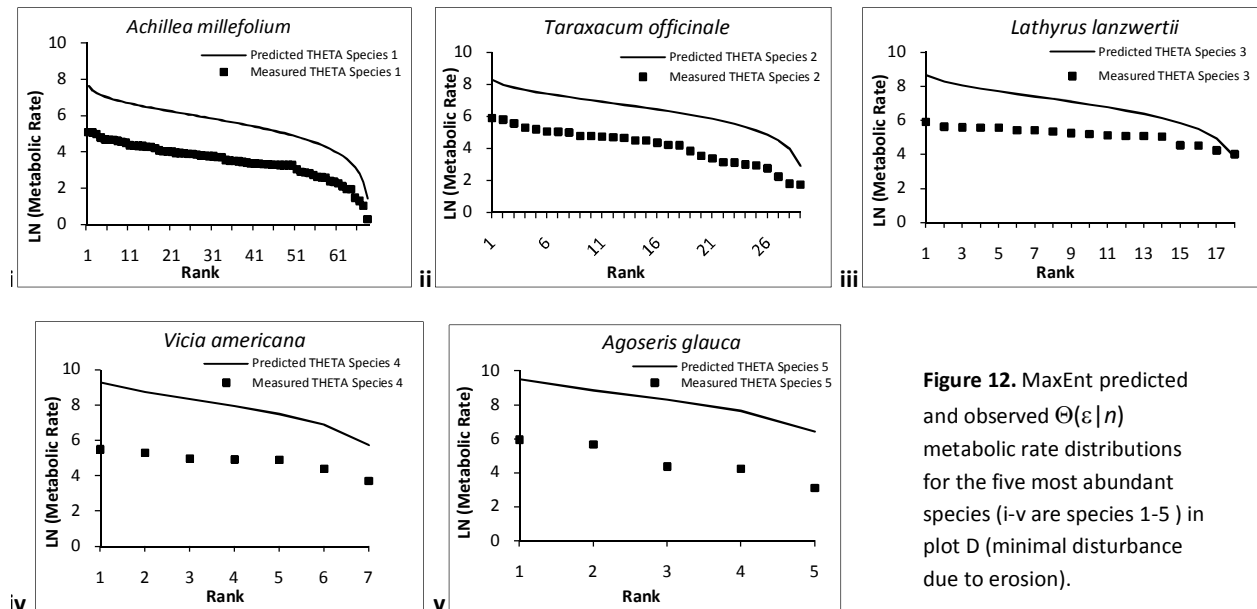


Figure 12. MaxEnt predicted and observed $\Theta(\varepsilon|n)$ metabolic rate distributions for the five most abundant species (i-v are species 1-5) in plot D (minimal disturbance due to erosion).

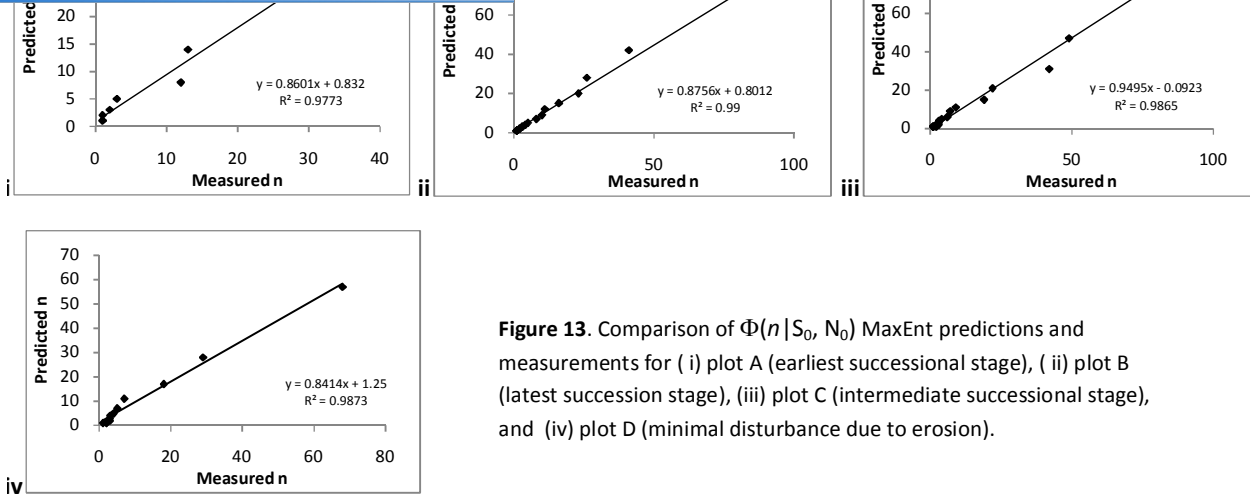


Figure 13. Comparison of $\Phi(n | S_0, N_0)$ MaxEnt predictions and measurements for (i) plot A (earliest successional stage), (ii) plot B (latest successional stage), (iii) plot C (intermediate successional stage), and (iv) plot D (minimal disturbance due to erosion).

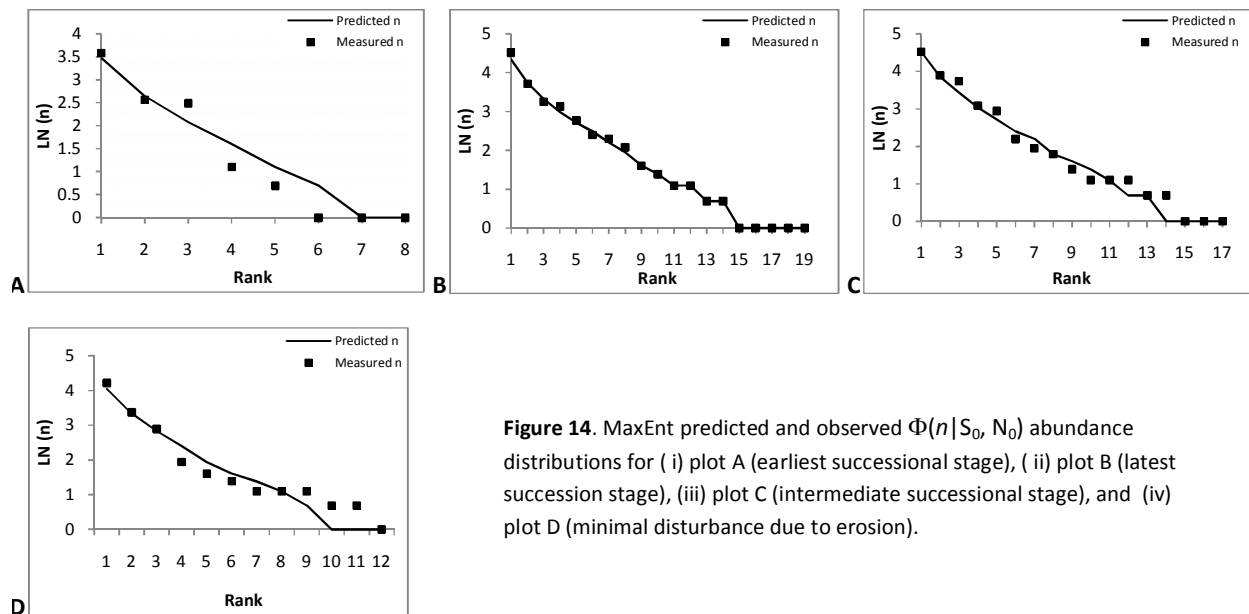


Figure 14. MaxEnt predicted and observed $\Phi(n | S_0, N_0)$ abundance distributions for (i) plot A (earliest successional stage), (ii) plot B (latest successional stage), (iii) plot C (intermediate successional stage), and (iv) plot D (minimal disturbance due to erosion).

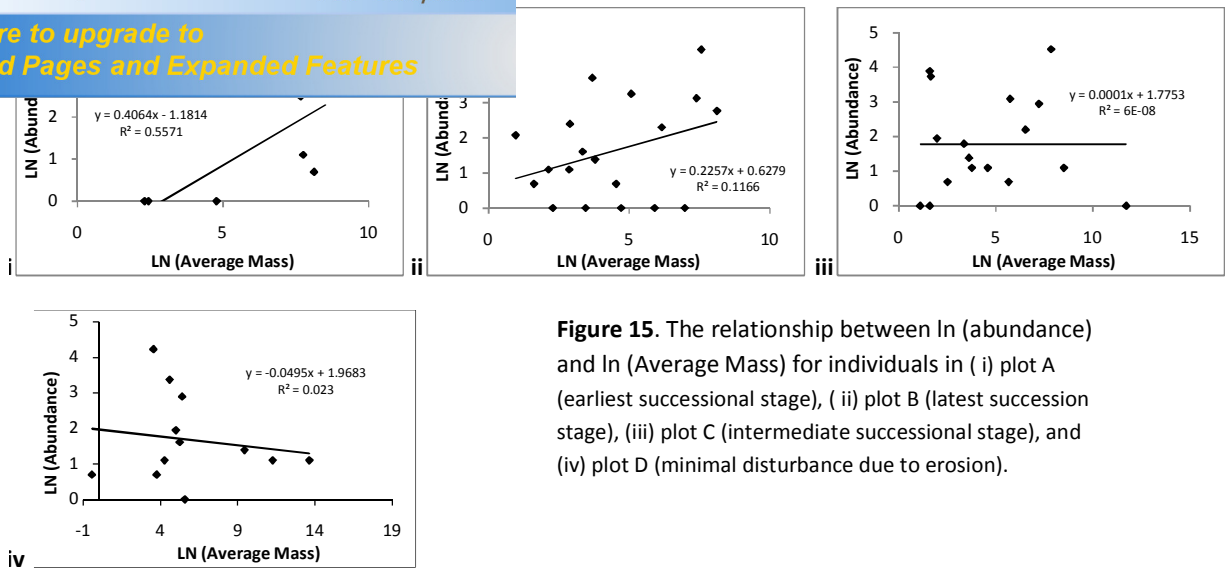


Figure 15. The relationship between ln (abundance) and ln (Average Mass) for individuals in (i) plot A (earliest successional stage), (ii) plot B (latest succession stage), (iii) plot C (intermediate successional stage), and (iv) plot D (minimal disturbance due to erosion).