

**A TEST OF SPECIES-AREA THEORY
ON A HIGH DISTURBANCE AREA OF THE GOTHIC EARTHFLOW**

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ABSTRACT

The species-area relationship (SAR) is a widely used concept in ecology, yet there is much controversy over its form. It has traditionally been assumed either to have a simple universal power-law form, $S = cA^z$, or to be idiosyncratic, varying from habitat to habitat, taxa to taxa, and spatial scale to spatial scale. Recently, a non-power-law, yet universal, form of the SAR has been derived from the maximum entropy principle. It has been shown to predict well the shapes of SARs across habitats, taxa, and spatial scales, and to allow estimation of species richness at biome scale from small plot data. All prior tests of this new theory have been conducted in relatively undisturbed habitats. This study tests the theory in a highly disturbed habitat on the Gothic Earthflow. While the theoretical prediction, based on 1 m² data, for species richness in the entire 256 m² plot was 37% lower than the measured richness, the slope values from the disturbed plot fell within the cluster of values taken from various undisturbed sites, and all followed the predicted curve fairly closely. The underestimate of large-scale species richness may result from statistically dynamic SAR slopes during the early stages of succession on a disturbed site. Further studies along successional gradients are needed to understand better the degree to which maximum entropy theory can be applied to disturbed habitats.

KEYWORDS

species-area relationship, power law, abundance, species richness, biodiversity, maximum entropy, scaling, macroecology

INTRODUCTION

The species-area relationship (SAR) describes the rate of increase in the number of species as area increases, and has long been a central concept in conservation biology and macroecology (Rosenzweig 1995). According to classic theory, the equation used to predict SAR was a power law function: $S=cA^z$, in which S represents the number of species within an area (A), and c and z are constants, with $z \approx 1/4$. Properties of the SAR were said to be affected by the sampling scheme, spatial scale, and types of organisms and habitats studied (Carey 2006). Over large scale ranges, the traditional SAR formula has been shown to break down, with fitted z values deviating both well above and well below $1/4$. More recent studies have provided a universal SAR formula that is derived from the maximum entropy (MaxEnt) principle from information theory and has been shown in various undisturbed habitats to more accurately predict

large-scale SARs, across a range of habitats, taxa, and spatial scales. In this theory, the shape of the SAR is calculated by solving (numerically) two simultaneous equations (Eq. 1, Eq. 2). Each solution gives species richness at a doubled spatial scale, so the full SAR is derived by repeatedly solving the pair of equations over the full scale range.

$$\frac{N}{y} \sum_{n=1}^N \frac{e^{-xn}}{n} = \sum_{n=1}^N e^{-xn} \quad \text{Equation 1}$$

$$S(A) - ye^x + N \left(\frac{1 - e^{-x}}{e^{-x} - e^{-x(N+1)}} \right) \left(1 - \frac{1}{N+1} e^{-xN} \right) = 0 \quad \text{Equation 2}$$

Here x is a “Lagrange multiplier,” a parameter determined from the MaxEnt machinery. $S(A)$ is the known value of species richness at some scale A , and y is the value of $S(2A)$ that is sought. N is twice the measured value of total abundance at scale A , which, because of the nested design of the SAR, is also the value of abundance at scale $2A$ (Harte et al. 2009).

Until now the universal SAR derived from MaxEnt has not been tested in disturbed habitats. The purpose of the current project is to see how well this theory performs in a highly disturbed site and to compare that performance with the accuracy of its predictions in studies of various undisturbed habitats. The search for a high disturbance site led to the Gothic Earthflow, located in the East River valley about 4 km south of the old mining town of Gothic, Colorado. The earthflow is said to have occurred in 1923 and involved both a flowage of surface earth and a downward slippage, or slump, of a mass of substratum. This resulted in a highly disturbed area about 1 km wide and 2 km long (Langenheim 1956, Curtin 1993). Even after 85 years, the Gothic Earthflow is clearly visible in satellite photos of the area (Photo 1). Today the area is still only sparsely revegetated (Photo 2), and this fact makes it an appropriate disturbance site upon which to test the universal SAR.

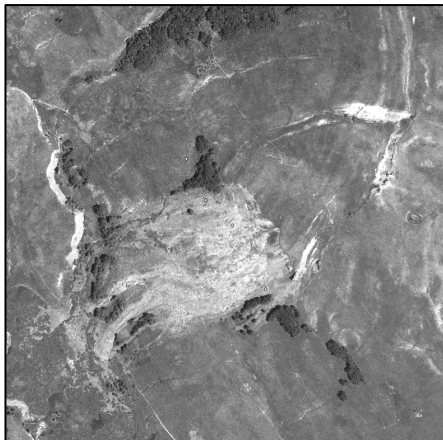


Photo 1: Satellite Photo of Earthflow

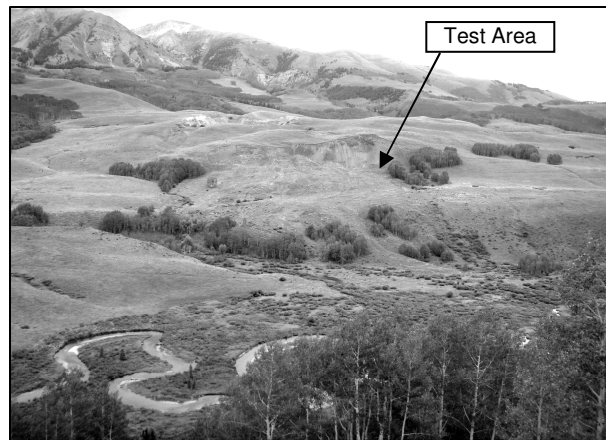


Photo 2: Earthflow Viewed from Gothic Road

My question is this: will the universal SAR derived from MaxEnt accurately predict the measured SAR on disturbed sites? Testing this is important because accurate predictions of SARs are valuable to disturbance ecologists who deal with the very important issues of land conservation and preservation of biodiversity.

METHODS

The test plot was located in the upper third of the Gothic Earthflow. This area was chosen because it is a severely disturbed area, as shown by the fact that percent cover there was calculated to be 19.2%. A 16m x 16m plot was laid out and then subdivided into 256 square-meter cells using stakes and string. All living plants in each square-meter cell were identified and counted, with each species listed, along with the number of individuals found. Each species was identified as accurately as possible with the information available. While some error may have occurred in species identification, such error would not affect the final outcome of this project because the important requirement for data collection was that different species be counted separately, regardless of identification. (A complete species list, along with abundance data, is found in the Appendix.) Plants that grow in obvious clumps were listed as one individual per clump, and were counted in the cell where the majority of its roots were located. Size and maturity were not a consideration during data collection, except that plants under 1 cm in height were not counted because of the difficulty in identification. All grasses and sedges were excluded for the same reason. These exclusions have no effect on the predictions of the universal SAR derived from MaxEnt, which has been shown, both theoretically and experimentally, to accurately predict SARs for any pre-defined group of organisms (Harte et al. 2009).

The averages of species richness and abundance at the 1m x 1m scale were plugged into the given SAR equations (Eq. 1, Eq. 2) using MathCad to predict the SAR at the 16m x 16m scale. The observed SAR was plotted using the average species richness from field measurements at the following scales: 1 m², 4 m², 16 m², 64 m², and 256 m². The measured SAR was then compared to the predicted SAR using a linear regression in a ln-ln graph (Fig. 1). The slope calculations from the measured data were also placed into a scatter graph along with data from several undisturbed test sites to be compared with the slope predicted by the theory (Fig. 2).

RESULTS

This study was concerned with species richness and abundance data collected from the Gothic Earthflow. Summary statistics are given in Table 1. The

averages were placed into the equations derived from MaxEnt (Eq. 1, Eq. 2) to make the predictions necessary to perform the desired tests.

DATA COLLECTED FROM GOTHIC EARTHFLOW TEST PLOT	
Total species (richness) in 16m x 16m plot	27
Total individuals (abundance) in 16m x 16m plot	1626
Average number of species (richness) in 1m x 1m cell	2.301
Average number of individuals (abundance) in 1m x 1m cell	6.352

Table 1

The first test involves the species richness prediction. The richness predicted by the theory for the 256 m² scale was 17, while the measured richness was 27 (Fig. 1). The prediction was lower than the measured result by 37%. This ecologically significant difference indicates that the universal SAR derived from MaxEnt does not accurately predict richness in a high disturbance area.

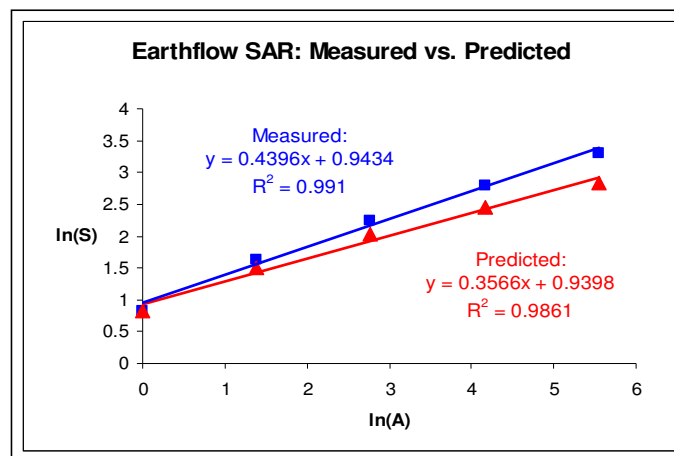


Figure 1

The second test is a bit more complicated. The universal SAR formula derived from MaxEnt expresses the local slope, $z(A)$, of the SAR as a function of N/S at any scale, A , with N equal to the species abundance and S equal to the species richness at that scale. The test involves plotting the slope of the species-area curve against $\ln(N/S)$. The theory predicts a unique curve on such a graph (Fig. 2, Harte et al. 2009). The accuracy of its prediction has been tested in undisturbed habitats by plotting the slope values derived from measured data in several different test sites. Adding the values from the Gothic Earthflow to the graph shows that the values from this high disturbance site fall within the cluster formed by all the values from the various undisturbed sites. Visual inspection indicates that the Earthflow data do not deviate from the predicted line anymore

than do data from undisturbed sites. It is interesting to note that the values from the Earthflow lie above the line as do the values from the serpentine grassland, another sparsely-vegetated area of poor soil.

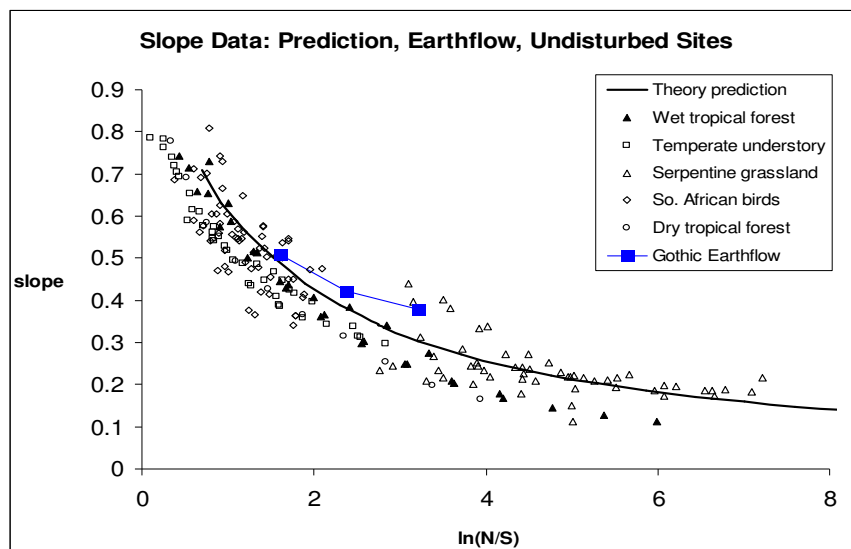


Figure 2

DISCUSSION

The results of the two tests lead to slightly different conclusions. The predicted SAR underestimates large-scale species richness from very small-scale data in a highly disturbed area as compared to its more accurate predictions for undisturbed areas. However, its slope predictions encompass measured data from both disturbed and undisturbed sites.

One possibility for the discrepancy between the measured and predicted SARs is that SAR slopes may be statistically dynamic throughout the various stages of succession while a site is recovering from disturbance (Carey 2006). Previous studies on the Gothic Earthflow have documented significant changes in species diversity and abundance over different periods of succession. (Langenheim 1956, Turbak 1969). In such a sparsely-vegetated stage of recolonization as is the test site on the Gothic Earthflow, there may be more space available to a greater diversity of species for exponential growth. As time passes and the number of individuals per square meter increases, some species may be entirely crowded out as only the better-adapted species survive and thrive. If this were true, it would result in a lower value for species richness as the site progresses into later stages of succession.

So we see how this study confronts directly the ambiguity that can arise in determining the success of a theory. The data in Figure 2 suggest that the MaxEnt theory is successful when applied both to the many undisturbed habitats

in which it has previously been tested and to the disturbed habitat at the Gothic Earthflow. The figure indicates that the central tendency of observed SAR slopes follows the MaxEnt prediction equally as well for this disturbed habitat as for many undisturbed habitats. On the other hand, Figure 1 indicates that the theory underpredicts by 37% species richness at the earthflow at the 256 m² scale using the data from 1 m². Thus, while the theory predicts the observed general tendency of the SAR slopes for disturbed and undisturbed sites equally well, it fails the test of accurately predicting species richness at large scales on the disturbed site. Similar failures to accurately upscale species richness have been noted at some, but not all, of the undisturbed sites (Harte et al., 2009).

Further studies on a variety of high disturbance sites, in various stages of succession, are necessary to understand more fully the degree to which a universal SAR derived from maximum entropy theory can be applied to disturbed habitats. I hope that this preliminary test may serve to provide inspiration as well as a sense of direction for such future tests.

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APPENDIX

Species List in Order of Abundance
on 256 m² Test Plot on the Gothic Earthflow

Species Name	Abundance
<i>Linaria vulgaris</i>	538
<i>Heterotheca villosa</i>	473
<i>Eriogonum umbellatum</i>	177
<i>Chrysothamnus nauseosus</i>	145
<i>Galium boreale</i>	44
<i>Artemisia dracunculus</i>	36
<i>Ipomopsis aggregata</i>	30
<i>Arnica longifolia</i>	25
<i>Eriogonum coloradense</i>	24
<i>Taraxacum officinale</i>	21
<i>Artemisia tridentata</i>	19
<i>Erysimum asperum</i>	13
<i>Erigeron speciosus</i>	13
<i>Castilleja linariifolia</i>	12
<i>Chaenactis douglasii</i>	11
<i>Linum lewisii</i>	10
<i>Symphoricarpos albus</i>	9
<i>Viola nuttallii</i>	8
<i>Potentilla gracilis</i>	6
<i>Lupinus argenteus</i>	3
<i>Phacelia heterophylla</i>	3
<i>Arabis glabra</i>	1
<i>Arnica mollis</i>	1
<i>Frasera speciosa</i>	1
<i>Valeriana occidentalis</i>	1
Unknown 1	1
Unknown 2	1