

# The Unimodal (Species Richness-Biomass) Relationship in Microcommunities Emerging from Soil Seed Banks

**Michael W. Palmer**

Department of Botany, Oklahoma State University, Stillwater OK 74078

**Mumtaz Hussain**

Department of Botany, University of Agriculture, Faisalabad, Pakistan

**We propose using plant microcommunities emerging from soil seed banks as experimental systems for studying species richness. We gathered soil from four Oklahoma terrestrial habitats, kept the soil moist in pots in a greenhouse, and allowed plants to germinate and interact under different conditions. Although heterogeneity among samples was minimized, we observed the often-reported unimodal relationship between richness and biomass in several habitats and treatments. ©1997 Oklahoma Academy of Science**

## INTRODUCTION

The relationship between species richness and above-ground biomass is emerging as a central theme in diversity studies (1-8). This relationship appears to be unimodal in many systems, with richness peaking at intermediate levels of biomass. Explanations for this unimodal relationship vary, but usually involve the existence of an underlying productivity or disturbance gradient (e.g. 9-11). For example, at very low productivity or high disturbance, few species can survive; hence, richness is low. Alternatively, at low biomass there tend to be few individuals, and hence, as a sampling artifact, few species exist (12,13). At high productivity or low disturbance, one or a few species can monopolize the available resources and thereby competitively exclude other species. It is only at intermediate levels of productivity or disturbance that richness is capable of reaching a peak.

At least two factors can confound detecting a unimodal richness relationship. The first confounding factor is the presence of external environmental variables (14). It is difficult to control for environmental heterogeneity in the field, because such variation is effectively hidden (15-17). Even if the most important environmental variables are not hidden, it is possible that both richness and productivity respond strongly but independently to those environmental variables, leading to a false conclusion of a causative relationship between richness and biomass. A second factor confounding the relationship between richness and biomass is that communities often contain a mixture of annuals and perennials, and these two groups may have fundamentally different responses to productivity (18).

Ecologists have successfully used microcommunities of plant species that emerge from soil to elucidate the nature of the soil seed bank (e.g. 19-23). In such experiments, investigators typically remove seedlings after they identify and count them. However, if the plants have the opportunity to grow and interact, we believe that such microcommunities also hold a promise for understanding the regulation of diversity. Such microcommunities can potentially become a *Drosophila melanogaster* of community ecology because they are small and are easy to replicate and manipulate. In particular, by thoroughly mixing soil samples, it is possible to minimize environmental heterogeneity among samples. Also, because the microcommunities initially have zero above-ground biomass, productivity will be equivalent to standing biomass.

This paper describes the results of an experiment on microcommunities arising from soil that was taken from a number of differ-

ent habitats, and which was subjected to several different treatments. Although the overall objectives of this research include comparisons of species richness, species composition, and life history patterns among habitats and treatments, this paper has a more modest aim to determine whether or not a unimodal richness-biomass relationship emerges spontaneously, even in the absence of environmental heterogeneity.

## METHODS

There were two phases to this research: Experiment I, which involved a comparison among habitats, and Experiment II, which involved clipping and fertilization treatments.

For Experiment I, on May 14, 1992, we collected 50 soil samples from each of four habitats (a roadside, a floodplain forest, a tallgrass prairie, and an oldfield) in the Nature Conservancy's Tallgrass Prairie Preserve, Osage County, Oklahoma. Soil samples measured  $20 \times 20$  cm, were 3 cm deep, and were randomly located within a  $30 \times 30$ -m plot in each habitat except for the roadside, in which the plot measured  $300 \times 3$  m. For processing soil samples, we followed the methods of Thompson and Grime (24), Lavassor et al. (25), and Ingersoll and Wilson (26). We dried the soil in thin layers on metal trays in the dark, and then gently passed the samples through 1-cm<sup>2</sup> mesh to remove stones and large plant fragments. We placed the soil samples for each habitat in the dark at room temperature for one month to break dormancy (27,28).

On June 14, we filled 40 plastic pots, measuring  $10 \times 10 \times 5$  cm, with thoroughly mixed soil from each habitat. Therefore, we had 40 pots consisting of mixed roadside soil, 40 pots of mixed floodplain forest soil, 40 pots of mixed tallgrass prairie soil, and 40 pots of mixed oldfield soil. We also filled an additional 40 pots with thoroughly mixed soil that was a composite of all four habitats. We then arranged the 200 pots in a randomized grid on a greenhouse bench, and kept the soil surface moist throughout the study period. We harvested the above-ground vegetation in all 200 pots three times: on August 14, October 14, and December 14, 1992. After each harvest, we dried the above-ground vegetation in an oven, identified and sorted the species, and weighed them. The species that emerged after each harvest included new recruits from the seed bank as well as individuals resprouting from below-ground parts.

For Experiment II, on May 14, 1993, we gathered 50 soil samples from the same locations, and used the same methods for collecting and drying the soil as for Experiment I. We thoroughly mixed the soil from all sites together and placed the soil in 320 greenhouse pots. On June 14, 1993, we divided the pots equally among four treatments: fertilized and clipped, clipped and not fertilized, fertilized and not clipped, and neither fertilized nor clipped, and randomly located the pots on two greenhouse tables. Because the block effect of the table was never important in this study, it is ignored throughout the rest of the paper. We imposed treatments on July 14, 1993. Clipping consisted of removing, with the aid of scissors, all plant material above 1 cm; and fertilization consisted of applying a time-released NPK fertilizer at the rate of 400 kg ha<sup>-1</sup>. We harvested the products of all treatments on August 14, 1993, and processed the vegetation as in Experiment I.

There is no straightforward way to test whether any given relationship between two variables is unimodal. One reason for this assumption is that many (theoretically, an infinite number of) formulae can model such a relationship. Without a very large sample size, it would be difficult to distinguish statistically between the models. We therefore chose to model the richness-biomass relationship with what are arguably the two simplest unimodal models: (1) a quadratic (parabolic) function

$$\text{Species richness} = b_0 + b_1B + b_2B^2 + \varepsilon$$

where  $B$  is the biomass,  $b_0$ ,  $b_1$ ,  $b_2$  are regression constants calculated by multiple linear regression (MLR) using the linear least-squares method, and  $\varepsilon$  is the error between

model and observation; (2) a Gaussian function:

$$\text{Species richness} = \varepsilon^{b_0 + b_1 B + b_2 B^2} + \varepsilon$$

calculated using Generalized Linear Modelling (GLM) with a Poisson error distribution and a logarithmic link function (29,30). We calculated MLR using Systat for Windows (30) and GLM using GLIM 4 (31). We chose to perform GLM in addition to MLR because each has advantages and disadvantages. First, MLR allows predicted values of species richness to be negative. Second, MLR assumes a normal error distribution. Because species richness is a count, it is more likely to have a Poisson error distribution. GLM solves these problems, but introduces new ones: (1) the calculation of an overall measure of goodness-of-fit such as  $R^2$  is problematic, and (2) the deviance statistic which assesses the significance of regression coefficients is asymptotically chi-squared, but it is not known how closely moderate-sized data sets approach the asymptote (32,33).

In both kinds of regression, a negative value for  $b_2$  describes a concave-down (i.e. unimodal) curve, and because the null hypothesis is that  $b_2$  is nonnegative, we took a significant ( $p < 0.05$ , one-tailed test) negative coefficient for  $b_2$  as evidence for a unimodal richness- biomass relationship. We use a one-tailed test. However, we have reported the results of the 2-tailed test because this test is the most conventional in MLR; a significant one-tailed test at  $p < 0.05$  is equivalent to a significant two-tailed test at  $p < 0.10$ . We were unable to find any reference as to how to perform a one-tailed test for regression coefficients for GLM; we suspect that because the Poisson error distribution is not symmetrical around the expected value, such a test is not simple. Thus, the two-tailed  $p$ -values we report for GLM should be taken as extremely conservative.

## RESULTS and DISCUSSION

Figure 1 illustrates the relationship between species richness and dry biomass for Experiment I. In all but one MLR (Table 1), and in all the Gaussian models (Table 2) the regression coefficient for the quadratic term was negative, leading to a concave-down and hence potentially unimodal curve. In all treatments except for the mixed soils, at least one of the harvests had a highly significant negative quadratic coefficient for both kinds of regression. Because the mixed soils in Experiment II, discussed later, exhibited significantly negative quadratic coefficients, we suspect the lack of significance in the mixed soils in Experiment I is probably due to chance variation or low statistical power, which in turn is due to a smaller sample size. In general, the peak in richness occurred within the range of the data points; if it had occurred outside of the range of the data, a significantly negative quadratic term could imply that richness levels off to a constant.

Some data points — those with zero biomass and, as a necessary consequence, zero species- are problematic; interpretation of the regression coefficients is difficult. In some respects, these empty pots can be considered perfectly valid observations, especially because a sampling effect has often been proposed to explain the increasing limb of the richness-biomass relationship (6,12,13). However, these points also introduce heteroscedasticity (the statistical problem of unequal variances, e.g. 34): not only is the mean number of species zero at zero biomass, but so is the variance. For those treatments that included some zero biomass observations, we recalculated both MLR and GLM regressions with such observations omitted. The results are at the bottom of Tables 1 and 2. Nine of the quadratic coefficients lose their statistical significance, and six even change from negative to positive, though never significantly so. However, we believe the unimodal relationship is a general pattern because (1) four of the treatments that had no observations with zero biomass had significant negative quadratic coefficients, (2) the third harvest of the prairie treatment remained highly significant in the MLR, and (3) a partial MLR of all the pots (not shown) using site and harvest as covariables, and also omitting all zero biomass values, had a very significantly negative quadratic coefficient ( $p < 0.0001$ ).

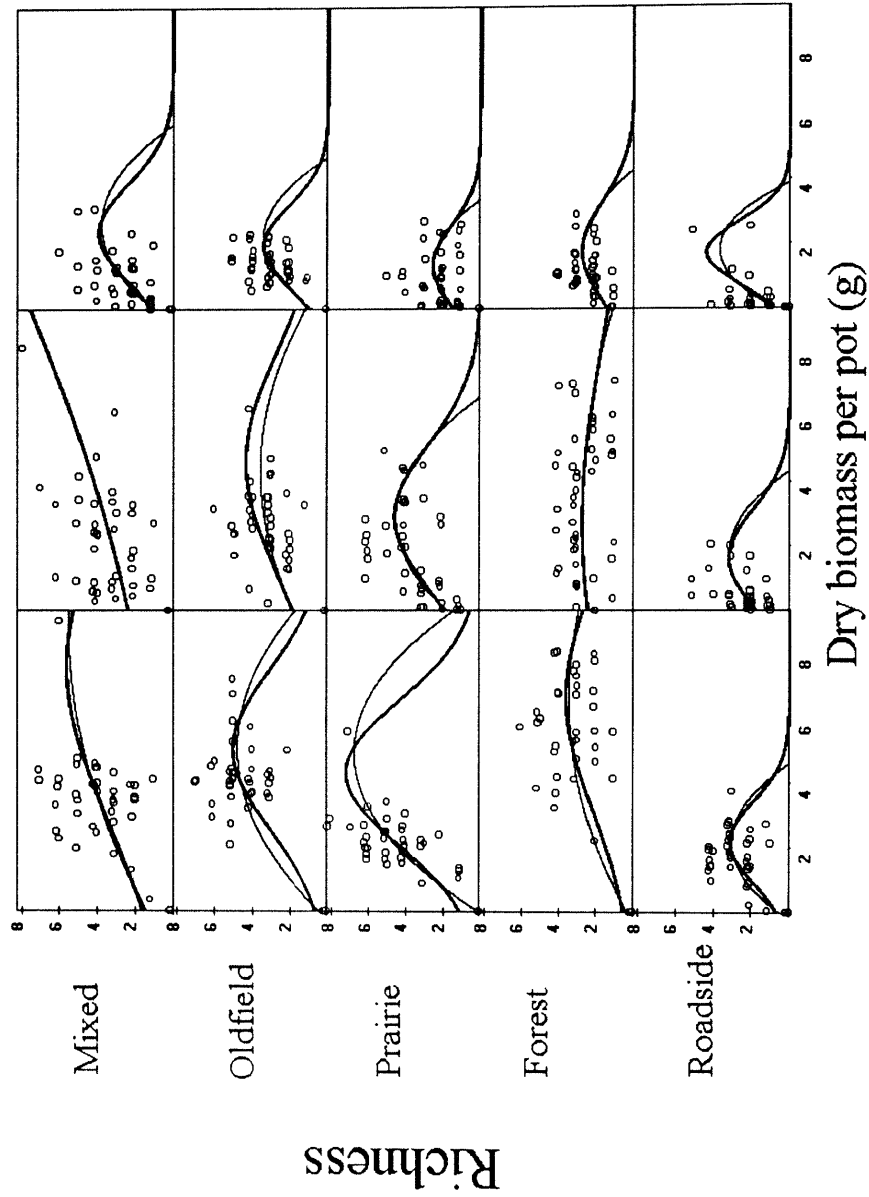


Figure 1. Experiment 1: Soil from four different habitats and all four habitats mixed together. Number of species as a function of dry biomass at three harvests for emerging plant microcommunities. Also shown are fitted quadratic curves (thin line) and Gaussian curves (thick line). We added a small random component to species richness to reveal overlapping data points.

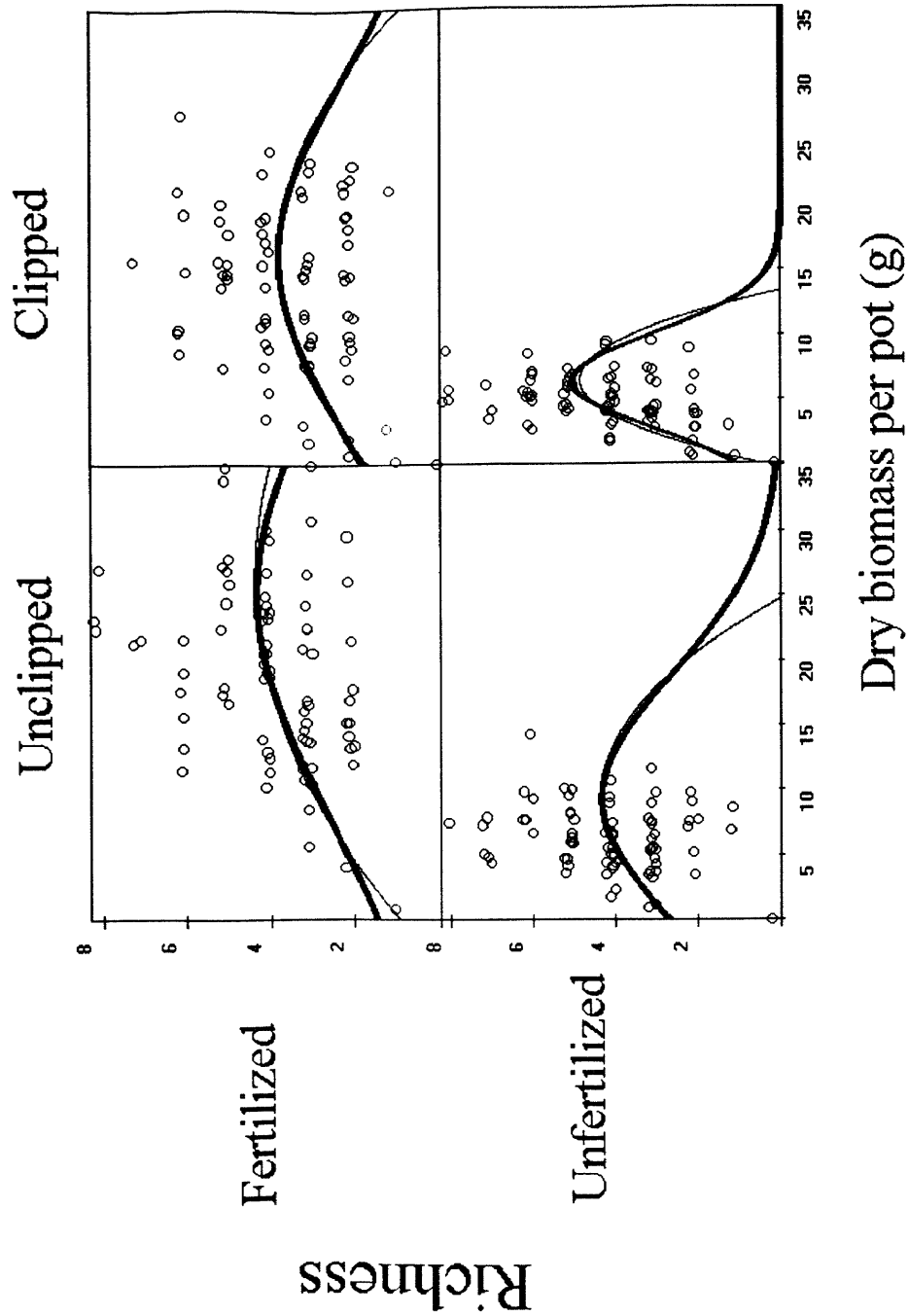


Figure 2. Experiment II: Mixed soil samples subjected to fertilization and clipping treatments. Number of species as a function of dry biomass for emerging plant microcommunities. Also shown are fitted quadratic curves (thin line) and Gaussian curves (thick line). We added a small random component to species richness to reveal overlapping data points.

TABLE 1. Experiment I: Linear Least Squares Regression Coefficients with the model: Species richness =  $b_0 + b_1B + b_2B^2 + \text{error}$ , with  $B$ =biomass.  $R^2$  is the multiple  $R^2$  for the entire model;  $N$  is the number of pots; H# indicates which of three harvests;  $p$ -values are calculated according to a 2-tailed test.

Source	H#	$N$	$b_0$	$b_1$	$b_2$	$R^2$
Roadside	1	40	0.5851	2.2182 <sup>e</sup>	-0.5093 <sup>e</sup>	0.454 <sup>e</sup>
	2	40	1.7226	1.6550	-0.4763	0.184 <sup>b</sup>
	3	40	0.8695	3.1336 <sup>d</sup>	-0.8669 <sup>b</sup>	0.363 <sup>e</sup>
Forest	1	40	0.3434	0.9343 <sup>e</sup>	-0.0706 <sup>d</sup>	0.330 <sup>e</sup>
	2	40	2.4659	0.2061	-0.0374	0.040
	3	40	1.3746	1.5323 <sup>b</sup>	-0.4320 <sup>b</sup>	0.184 <sup>b</sup>
Prairie	1	40	0.0854	2.7138 <sup>e</sup>	-0.2746 <sup>b</sup>	0.418 <sup>e</sup>
	2	40	1.7992	1.8888 <sup>e</sup>	-0.3274 <sup>d</sup>	0.379 <sup>e</sup>
	3	40	1.4589	1.6694 <sup>b</sup>	-0.6229 <sup>b</sup>	0.145 <sup>a</sup>
Oldfield	1	40	0.4459	1.7206 <sup>e</sup>	-0.1692 <sup>d</sup>	0.474 <sup>e</sup>
	2	40	1.7812	0.8401 <sup>a</sup>	-0.0969	0.128 <sup>a</sup>
	3	40	0.8069	2.4131 <sup>a</sup>	-0.5501	0.206 <sup>b</sup>
Mixed	1	40	1.3909	0.9203 <sup>b</sup>	-0.0508	0.207 <sup>b</sup>
	2	40	2.3768	0.3875	0.0184	0.261 <sup>d</sup>
	3	40	1.0426	2.0886 <sup>c</sup>	-0.3961	0.354 <sup>e</sup>
Zeros Removed						
Roadside	1	36	1.6724	1.1631 <sup>a</sup>	-0.2765	0.090
	3	30	1.4878	1.3466	-0.2306	0.245 <sup>b</sup>
Forest	1	37	2.7323	0.1815	-0.0154	0.004
Prairie	1	39	0.1685	2.6566 <sup>b</sup>	-0.2662	0.310 <sup>d</sup>
	3	39	1.5960	1.4401 <sup>b</sup>	-0.5502 <sup>b</sup>	0.113
Oldfield	1	37	6.9588	-1.0480	0.1082	0.026
	2	39	2.6926	0.2808	-0.0207	0.029
	3	39	2.6021	-0.0520	0.2201	0.084
Mixed	1	39	2.2052	0.5792	-0.0204	0.113
	2	38	3.0878	-0.0290	0.0647	0.228 <sup>b</sup>
	3	36	1.6044	1.2674	-0.1684	0.221 <sup>b</sup>

a.  $p < 0.10$ ; b.  $p < 0.05$ ; c.  $p < 0.01$ ; d.  $p < 0.005$ ; e.  $p < 0.001$

The results of Experiment II are displayed in Figure 2, and the regressions are summarized in Tables 3 and 4. All the regressions had a negative quadratic coefficient, and for three treatments the coefficients were statistically significant. The peak in richness in the regression curves of the fertilized treatments occurred at high levels of biomass, so it is possible that the true relationships are not actually unimodal but asymptotic. When those observations with zero biomass are removed, the significantly negative coefficients remained significantly negative, although not always by the more conservative, two-tailed test. When the treatments were used as co-variables in a partial MLR, and observations with zero biomass were removed, there remained a highly significant ( $p < 0.0001$ ), negative coefficient for the quadratic term.

The results of both experiments suggest that plant microcommunities emerging from soil seed banks exhibit a unimodal relationship between species richness and biomass. It is extremely unlikely that this relationship is caused by underlying environmental heterogeneity, because conditions in the green-

TABLE 2. Experiment I: GLM Regression Coefficients calculated with a logarithmic link function and Poisson error distribution with the model: Species richness =  $e^{b_0+b_1B+b_2B^2}$  + error, with  $B$ =biomass. Significance is based on the chi-squared approximation of the deviance statistic (32). H# indicates which of three harvests;  $N$  is the number of pots; NS means  $p > 0.10$ .

Source	H#	$N$	$b_0$	$b_1$	$b_2$	Overall Model
Roadside	1	40	-0.3265	1.3470 <sup>d</sup>	-0.30910 <sup>c</sup>	<sup>d</sup>
	2	40	0.5771	0.7270	-0.22370	NS
	3	40	-0.0455	1.7840 <sup>b</sup>	-0.51990 <sup>a</sup>	<sup>c</sup>
Forest	1	40	-0.5331	0.5452 <sup>d</sup>	-0.04078 <sup>c</sup>	<sup>d</sup>
	2	40	0.8964	0.0856	-0.01550	NS
	3	40	0.3858	0.7196	-0.20360	NS
Prairie	1	40	0.1260	0.8616 <sup>d</sup>	-0.09989 <sup>b</sup>	<sup>d</sup>
	2	40	0.6839	0.5825 <sup>d</sup>	-0.09978 <sup>b</sup>	<sup>c</sup>
	3	40	0.4030	0.8331 <sup>a</sup>	-0.31090 <sup>a</sup>	NS
Oldfield	1	40	-0.3956	0.8025 <sup>d</sup>	-0.07957 <sup>d</sup>	<sup>d</sup>
	2	40	0.6432	0.3661	-0.03985	NS
	3	40	0.04895	1.223	-0.31220	NS
Mixed	1	40	0.5081	0.3219 <sup>b</sup>	-0.02112	<sup>b</sup>
	2	40	0.8684	0.1582	-0.00374	<sup>b</sup>
	3	40	0.1713	1.0160 <sup>c</sup>	-0.21370 <sup>a</sup>	<sup>c</sup>
Zeros Removed						
Roadside	1	36	0.5535	0.4897	-0.11640	NS
	3	30	0.4135	0.7085	-0.15370	NS
Forest	1	37	1.0140	0.0578	-0.00491	NS
Prairie	1	39	0.4250	0.6656 <sup>b</sup>	-0.07237 <sup>a</sup>	<sup>b</sup>
	3	39	0.4844	0.7010	-0.26880	NS
Oldfield	1	37	2.0210	-0.2203	0.02275	NS
	2	39	0.9981	0.0920	-0.00728	NS
	3	39	0.9308	0.0358	0.05332	NS
Mixed	1	39	0.8529	0.1828	-0.00927	NS
	2	38	1.0990	0.0329	0.00923	<sup>a</sup>
	3	36	0.5172	0.5592	-0.09343	<sup>a</sup>

a.  $p < 0.10$ ; b.  $p < 0.05$ ; c.  $p < 0.01$ ; d.  $p < 0.005$ ; e.  $p < 0.001$

house were relatively uniform and soil for each treatment was thoroughly mixed. The most plausible explanation for the observed patterns is that there is stochastic variation in the propagules present. Pots that by chance have more propagules of fast-growing species with a high competitive effect, or species at the top of a competitive hierarchy (35), will have high competitive exclusion rates, and hence low species richness, as well as high biomass. Pots with, by chance, very few seeds will have simultaneously a low eventual biomass and species richness. Pots that initially have a number of seeds of several species, but do not include a large number of species with high competitive effect, will tend to have an intermediate biomass and relatively high richness.

Although there are a large number of significant regressions, we must stress that the relationships are often quite weak, though no weaker than in many field studies. The values

TABLE 3. Experiment II: Linear Least Squares Regression Coefficients with the model: Species richness =  $b_0 + b_1B + b_2B^2 + \text{error}$ , with  $B$ =biomass.  $R^2$  is the multiple  $R^2$  for the entire model, and  $N$  is the number of pots.

Frtlzd <sup>f</sup>	Clpd <sup>g</sup>	$N$	$b_0$	$b_1$	$b_2$	$R^2$
No	No	80	2.6005	0.3639	-0.0190	0.053
No	Yes	80	0.4627	1.3475 <sup>e</sup>	-0.1037 <sup>e</sup>	0.291 <sup>e</sup>
Yes	No	80	0.9326	0.2605 <sup>c</sup>	-0.0049 <sup>b</sup>	0.151 <sup>d</sup>
Yes	Yes	80	1.6535	0.2613 <sup>d</sup>	-0.0080 <sup>b</sup>	0.123 <sup>c</sup>
Zeros Removed						
No	No	79	3.5035	0.1070	-0.0026	0.015
No	Yes	78	0.7630	1.2358 <sup>e</sup>	-0.0943 <sup>d</sup>	0.183 <sup>e</sup>
Yes	Yes	79	1.9858	0.2137 <sup>b</sup>	-0.0065 <sup>a</sup>	0.077 <sup>b</sup>

*a.*  $p < 0.10$ ; *b.*  $p < 0.05$ ; *c.*  $p < 0.01$ ; *d.*  $p < 0.005$ ; *e.*  $p < 0.001$ ; *f.* Fertilized; *g.* Clipped.

TABLE 4. Experiment II: GLM Regression coefficients calculated with a logarithmic link function and Poisson error distribution with the model Species richness =  $e^{b_0+b_1B+b_2B^2} + \text{error}$ , with  $B$ =biomass. Significance is based on the chi-squared approximation of the deviance statistic (32). NS means  $p > 0.10$ .

Frtlzd <sup>f</sup>	Clpd <sup>g</sup>	$N$	$b_0$	$b_1$	$b_2$	Overall Model
No	No	80	0.9987	0.10090	-0.005369	NS
No	Yes	80	0.1010	0.47490 <sup>d</sup>	-0.037140 <sup>d</sup>	<sup>d</sup>
Yes	No	80	0.3950	0.08569 <sup>b</sup>	-0.001674 <sup>a</sup>	<sup>b</sup>
Yes	Yes	80	0.6008	0.09120 <sup>b</sup>	-0.002788 <sup>a</sup>	<sup>b</sup>
Zeros removed						
No	No	79	1.2570	0.02827	-0.000771	NS
No	Yes	78	0.3979	0.36820 <sup>b</sup>	-0.028370 <sup>b</sup>	<sup>d</sup>
Yes	Yes	79	0.7459	0.07032 <sup>a</sup>	-0.002131	NS

*a.*  $p < 0.10$ ; *b.*  $p < 0.05$ ; *c.*  $p < 0.01$ ; *d.*  $p < 0.005$ ; *e.*  $p < 0.001$ ; *f.* Fertilized; *g.* Clipped.

for multiple  $R^2$  imply that at most, 47.4% (or more typically, 5% to 35%) of the variation in richness can be explained by a quadratic function of biomass. We attribute most of the remaining variation to stochastic variation in the initial seed pool, although we do not want to rule out the possibility of variation caused by interactions between species. Despite its weakness, the unimodal relationship appears to be repeatable enough to suggest that microcommunities emerging from soil seed banks are a promising system for future work on the nature of the richness-biomass relationship.

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