TAILORED VINES AND TAYLOR'S LAW:
Examining Vine Growth on Puerto Rican Coffee Farms

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Abstract

How to deal with weeds is one of the most persistent problems in modern agriculture. The goal of agroecologists generally, is not only to understand agricultural systems in an ecological context, but also to apply ecological principles in aiding farmers with potential problems, such as weeds. One such agricultural system is the coffee sector of Puerto Rico and the most evident weed problem is vines. We use simple ecological principles to understand the dynamics of vines that plague these coffee farms in Puerto Rico. The ecological tool we chose to use to this end is Taylor's Law (TL). Discovered by L.R. Taylor in the 1960s, TL states that there is a power law relationship between a population's size and its variance. Since its publication, L.R. Taylor's paper has spawned countless studies in various fields including ecology. We use TL in an attempt to understand the evident variability of vines on coffee farms. To do this, over a period of 12 months from August 2018 to July 2019, vine coverage on 20 coffee plants in 26 different coffee farms was sampled. We found that not only are both the temporal and spatial forms of TL present on these coffee farms, but that the Lewontin-Cohen model of stochasticity (LC) was also at play within this study system. The LC model postulates that a population's exponential rate of increase varies at random, independently of both the population's size and time. The combination of Taylor's Law and the Lewontin-Cohen model combine to explain both the general power law relationship between mean and variance and the deviation from the expectation of 1.0 for the parameter of that relationship. With these results, we hope that simple ecological laws will be able to help with weed management in agricultural systems.

Vines as Weeds

There are times when nature presents us with roadblocks that curtail desired activities. One such roadblock, recognized since antiquity, is the antagonistic effects of pests in agriculture. Although historically this problem has been approached with something akin to a sledgehammer rather than a scalpel, in 1997 a group of establishment entomologists challenged this epistemological bias with a game-changing article entitled, "A total system approach to sustainable pest management" where they state:

> "We must turn more to developing farming practices that are compatible with ecological systems and designing cropping systems that naturally limit the elevation of an organism to pest status. We historically have sold nature short…" (Lewis *et al*, 1997)

In short, their counsel is to employ ecological principles in the development of management tools for dealing with these preeminent examples of nature's roadblocks – agricultural pests. With an eye towards the particular question of weed control, one of the more persistent problems of agriculture, and plant ecology, has been elaborating the ecology of weeds.

One example of weed management as a persistent problem can be observed on the coffee farms of Puerto Rico, which are also home to many types of vines. There are approximately 386 native species of climbing plants in Puerto Rico and the Virgin Islands, of which 274 are native (Acevedo-Rodriguez, 2005). Vines are climbing plants that are rooted in the soil, but which require external aid for their stems to remain erect. One way of being erect and reaching sunlight is by growing on other plants (Acevedo-Rodriguez, 2005). On coffee farms, vines can use coffee plants to help with vertical growth, and, when not controlled, can cover the entire plant reducing its photosynthetic capacity. Therefore, most vines are considered weeds on Puerto Rican coffee farms.

In order to develop a total system approach to vine management in coffee farms, we need to understand the ecology of these plants. One particular component of theoretical ecology that stands out both for its obvious potential applicability and its relative scarcity in the agroecological literature is Taylor's law of fluctuation scaling. Taylor's law is a well-verified statistical reality that applies to a variety of circumstances and, we argue, has great potential for creating a background theory for understanding the problem of vines as weeds in agriculture. Thus, the main aim of this paper is to analyze the presence of Taylor's Law with respect to vine growth in coffee farms in Puerto Rico in order to gain insights that can help in designing a total system approach to weed management. Furthermore, we examine differences in the presence of TL according to the management style related to tree canopy shade cover of the farms.

Taylor's Law of Fluctuation Scaling

Taylor's Law is a phenomenon seen in complex systems across many different fields of research, ranging from engineering sciences, to physics, sociology and biology. Named after L.R. Taylor who presented it in a 1961 paper on natural populations, this "law" broadly states that there is a power law relationship between a population's size and its variance. In other words, for a fixed species and/or population, population variance (V) can be written "as a constant (b) times the average population (M) to a power α" (Taylor, 1961; Eisler *et al*, 2008), i.e.

$$V = bM^{\alpha} \qquad\qquad [1]$$

The parameter α is the slope of the linear regression on a log-log scale of population mean and variance (Ong *et al*, 2020), and it tends to fall between 0 and 2 for populations of living organisms (Eisler *et al*, 2008). This simple power law relationship between population size and

variance is an important tool in characterizing population variability (Eisler *et al*, 2008; Cohen *et al*, 2012; Ong *et al*, 2020).

There exist two main forms of TL: spatial and temporal, with the spatial form commonly referred to as *ensemble* (Eisler *et al*, 2008; Fronczak & Fronczak, 2010). In the temporal form, the variance of abundance of a population over time will follow a power law relationship to the abundance mean over the same time frame (Ong *et al*, 2020), while the spatial form looks at how the variance through space follows the power law relationship to the population mean (Eisler *et al*, 2008). Both forms have been observed in ecological research, such as with the population growth of plants.

The Process of Vine Growth

One of the questions in plant ecology is how plants, such as vines, grow. We presume that a plant, starting from some random biomass and at some initial point in time, will experience an exponential increase in biomass over time, frequently summarized with the recursion equation:

$$x(t + 1) = rX(t) \qquad [2]$$

Where $x(t)$ is the biomass of vines at time t. Given this equation, an exponential distribution is expected among a group of plants that started from random biomasses. With this assumption (equation 2), we can extrapolate the expected parameter of Taylor's Law for a given population:

$$mean\ (x) = \frac{1}{\lambda} \qquad [3]$$

$$variance\ (x) = \frac{1}{\lambda^2} = \left(\frac{1}{\lambda}\right)^2 = [mean\ (x)]^2 \qquad [4]$$

This is the same form as the TL equation (equation 1). Thus we have the linear function:

$$\ln[variance(x)] = \ln[mean(x)]^2 \qquad\qquad\qquad [5]$$

Or

$$\ln[variance(x)] = 2\ln[mean(x)] \qquad\qquad\qquad [6]$$

Thus, the variable x should follow TL with a α value of 2. This means that by presuming exponential growth within the vine populations on each of the bushes on the 22 coffee farms, we expect the expected slope for TL to be 2 when using variance, or 1 with standard deviation. Thus, by using a log-log graph of population mean and standard deviation, we have two criteria for establishing the presence of TL in our study system:

    I.   a high R^2 value (indicating a good fit of the regression prediction to the data)

    II.   a consistent slope (α) value of 1 with standard deviation

With this in mind, in this study we examine vine growth in coffee farms in Puerto Rico to determine if the spatial and temporal forms of TL can be detected. Since most of the vines that grow on coffee farms follow similar growth behavior (Perfecto *et* al, 2019), we do not distinguish between species but rather take vine growth in general.

Methods

Data collection for the project began in August 2018 in the coffee-production region of Puerto Rico, located in the west central part of the island (Figure 1). Researchers from the Vandermeer-Perfecto lab paid twelve monthly visits to 25 coffee farms in the area from August 2018 to July 2019. On each farm, a 10x10 m plot was established and 20 plants were randomly selected. Vine coverage percentage (regardless of vine species) of the 20 coffee plants was

estimated, once per month, with the same 20 coffee plants used for each farm throughout the 12 month period.
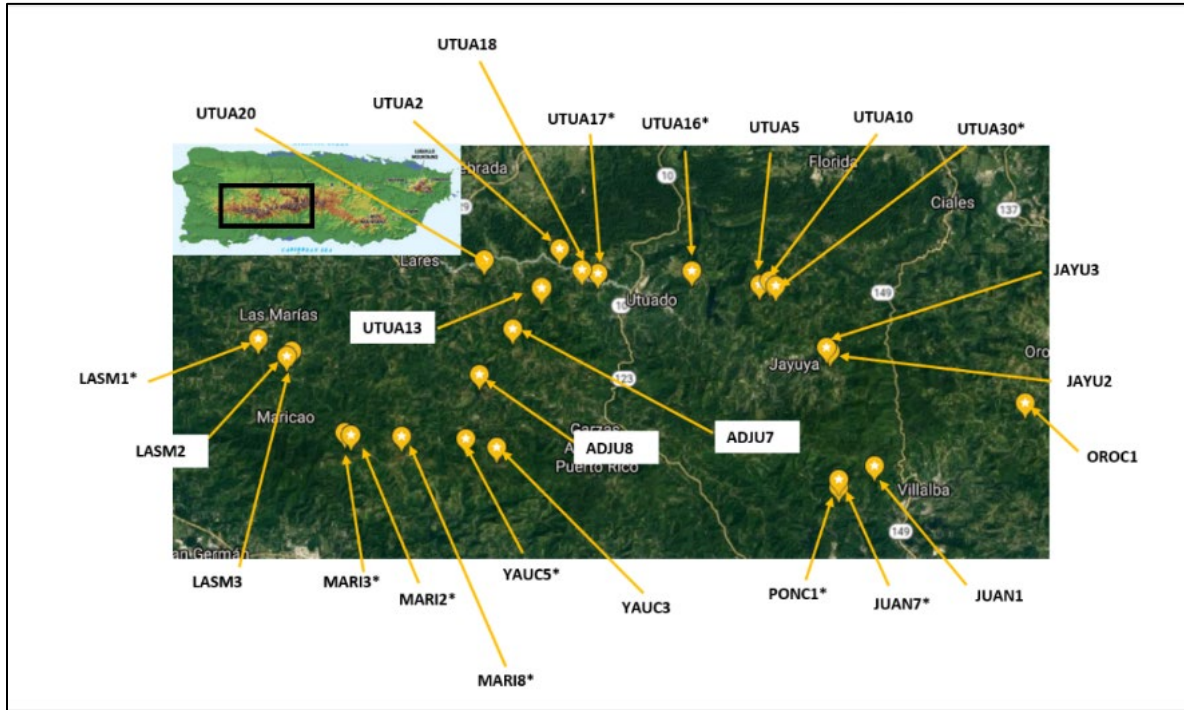

Figure 1: Map of the central coffee-production region of Puerto Rico, showing the locations of the coffee farms used in this study.

Analysis was done using Excel 2016, and included data for 22 of the 25 coffee farms. Some of the selected coffee plants on the other three farms were lost or uprooted, and researchers had to select new coffee plants to continue data collection. In order to have consistency in the data results, only the 22 farms with the same 20 coffee plants being used throughout data collection were used. In order to carry out a log-log graph of population mean and variance for both the spatial and temporal forms of TL for all 22 farms, we did the following calculations:

    I.   calculated the total vine coverage (TVC) of each farm

    II.   got the mean for spatial and temporal by dividing TVC by 20 (coffee plants) and 12 (monthly visits) for spatial and temporal respectively

III.   calculated standard deviation for all 20 plants/farm for spatial TL, and for all 12 monthly visits/farm for temporal TL

In addition, we also looked for the presence of TL in different farm subgroups, such as management style and change in vine coverage. Coffee farms in Puerto Rico have different management styles, which is usually seen on a gradient ranging from coffee monocultures with few to no shade trees, to diverse systems with forest-like canopy cover and lots of shade (Perfecto *et al*, 2019). In order to examine if shade management affected TL in any way (either R^2 and/ or the slope of the line), we classified each farm into three categories: 1) shaded farms, (farms that have shade trees in addition to coffee and plantains); 2) previously shaded farms (farms that were shaded before hurricane Maria, but after the hurricane, loss most of their shade trees; Hurricane María struck Puerto Rico in 2018, a year before the plots were established); 3) no-shade farms. This was done as we thought that having different management styles and/or changes in vine coverage would influence the presence of either form of TL.

Results

As seen in Figures 2 and 3, both the spatial and temporal forms of TL are evident in the vine growth on the 22 coffee farms, with the high R^2 values (approximately 96% for both). However, the α parameters are 0.74 and 0.72 for spatial and temporal data respectively, which are different from the theoretical value of 1. In addition, contrary to expectations, farms in the three different shade management categories had similar patterns regarding both forms of TL (Fig. S1 supplementary materials). Additionally, regardless of whether farms had experienced a change in vine coverage or not, a similar pattern for both forms of TL was also seen (Fig. S2 supplementary materials).
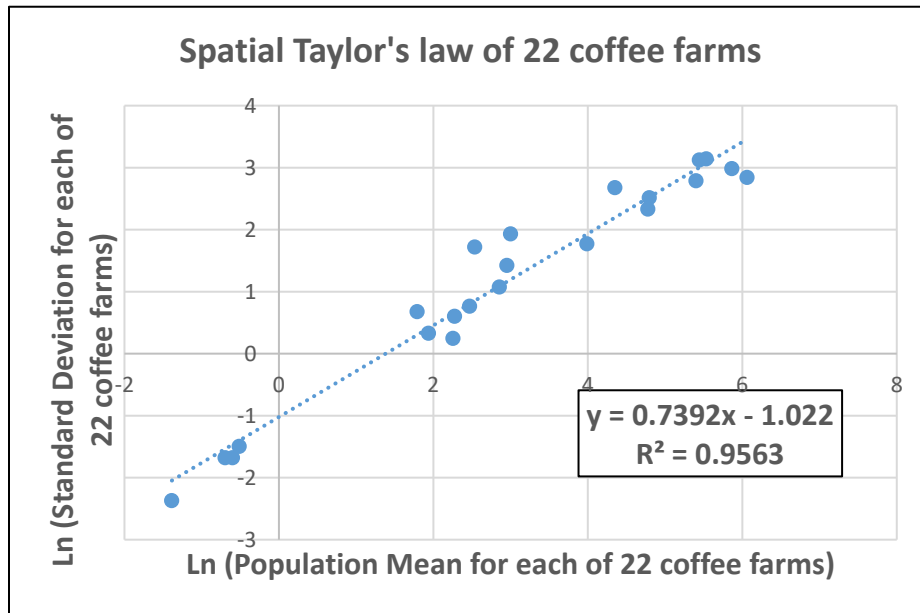
Figure 2: Initial Results of Spatial Taylor's Law, pooling data from all 22 farms.
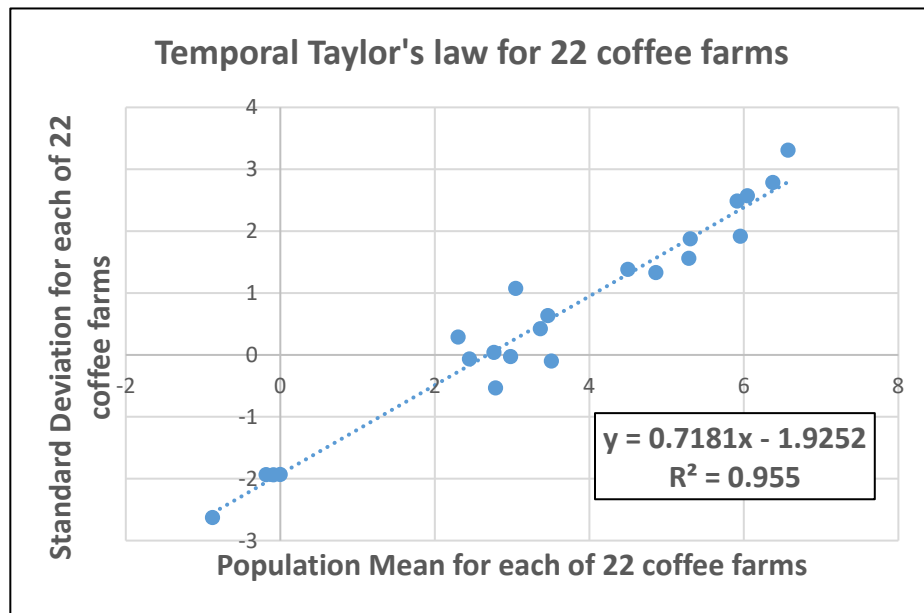

Figure 3: Initial Results of Temporal Taylor's Law, pooling data from all 22 farms.

Due to these similar patterns in our data, our next step was to look at TL separately for each sampling visit to see if there was a gradual emergence of TL as the growth of the vines proceeded (Figure S3 and S4 supplementary materials). We started at visit 2 onward, so we

could have variation in both time and space. Our findings show that both forms of TL were present from the beginning of the sampling period.

Our basic premise is that plants of similar groupings, say a group of vines on a particular coffee tree on a particular coffee farm, are expected to grow exponentially. That is, we expect that the vine growth on the 20 coffee plants on each of the 22 sampled coffee farms will be exponential, and TL will be present on each farm. To test this, we examined how many of the 22 coffee farms followed TL. Of the 22 farms only nine of them had sufficiently abundant vine growth to be subjected to this analysis. Detailed values of α and the R^2 for each of the nine farms for both forms of TL is provided in Table 1.

Furthermore, expecting exponential growth of the vines at least over short stretches of time, we took every 3 consecutive censuses at each farm and fit an exponential equation to approximate what might be the exponential parameter, assuming that vine growth is exponential over short periods of growth spurts. On each farm, all relevant triplets (i.e., three consecutive times a coffee bush had vines greater than the previous time) were treated in this way and the average exponential parameter was taken to be an estimate of the basic exponential growth of the vine community. If the fit to Taylor's law is a consequence of exponential growth of vine biomass, the slope of Taylor's law should be 1.0, as expected from theory.

Table 1: α, R^2 values, and exponential growth rate (and overall mean) of spatial and temporal TL for nine farms.

Farm	Spatial TL α	Spatial R^2	Temporal TL α	Temporal R^2	Exponential growth
LASM3	0.1408	0.1121	0.2343	0.3712	0.6418
UTUA10	0.5734	0.8473	0.4414	0.7086	0.7259
ADJU8	0.4422	0.761	0.6025	0.8353	0.6716
UTUA18	0.4422	0.761	0.6025	0.8353	0.6716
UTUA5	0.837	0.8952	0.6094	0.8494	0.6502
LASM2	0.6665	0.8963	0.6313	0.9136	0.7605
OROC1	0.5296	0.9232	0.7065	0.9536	0.5362
JUAN1	0.613	0.9386	0.7267	0.9443	0.7894
JAYU2	0.7784	0.8137	0.7902	0.9467	1.0287
Mean	0.6102875	0.8545	0.6388125	0.8734	0.7292625

Eight of the farms (excluding LASM3) had relatively high R^2 (> 0.5) values for both forms of TL, ranging from 0.71 to 0.95. The α slopes of the spatial and temporal forms of TL of all eight farms, however, were below the theoretical value of 1.

Discussion

By the measure of fit to a linear function in log-log space, we have strong confirmation of Taylor's law. But by the same theoretical token, the expectation of the value being 1.0 is violated. We propose that a way of explaining this deviation from theory value is contained within earlier literature on the effects of stochasticity on population growth.

Stochasticity can be defined as population growth where r, the exponential rate of increase, varies at random, independently of both population size and time (Lewontin & Cohen, 1969). In assuming that our empirical deviations in slope values are caused by stochasticity, we propose that the Lewontin-Cohen model (LC) of stochastic population growth will help explain

our results. With the LC model it is possible to predict and interpret Taylor's Law, as suggested earlier (Cohen *et al.*, 2013). As Cohen *et al.*, state:

> "The exponent of TL exceeds 2 if and only if the LC model is supercritical (growing on average), equals 2 if and only if the LC model is deterministic, and is less than 2 if and only if the LC model is subcritical (declining on average)…" (Cohen *et al*, 2013)

This means that in a system operating under the LC model, if no stochasticity is present then the TL α value should be equal to 1 with standard deviation on a log-log graph of population mean and variance The α value will be less than 1 if the model/population is declining, and will be greater than 1 if the model/population is increasing on average. This means that if the LC model is at play within our study system, our α value is less than 1 as our vine population is declining on average.

Stochasticity may be present in our system due to the weeding rate of the farmers and other environmental drivers such as local variability in microhabitat, plant pathogens and herbivores, etc. Thus, we postulate that the intrinsic growth rate of the vines is modified by a stochastic factor as proposed in the LC model. To see if our predictions were true, we carried out simulations of the vine growth using the LC model to see if they would give rise to the less than theoretical TL values seen in the empirical data. Simulations of the vines growing according to TL, but at different growth rates (r) and stochastic factor sizes are displayed in figure 4.
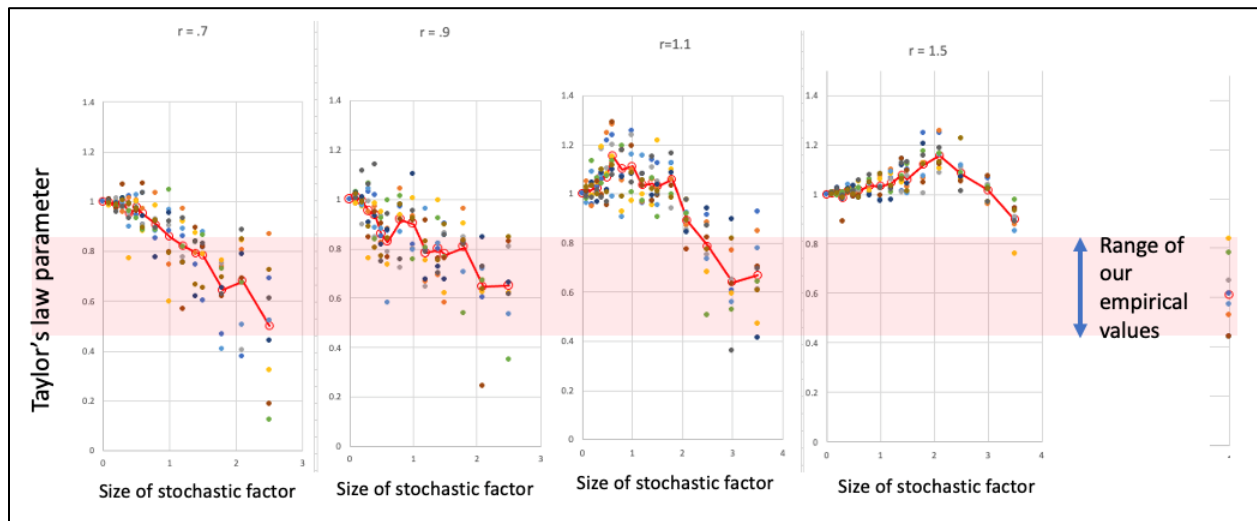
Figure 4: Simulations of Taylor's Law with varying sizes of stochastic factor for four values of the exponential parameter. Red, open circles represent mean α values of simulations run at a particular stochastic factor value.

As seen in Figure 4, our simulations revealed that when no stochasticity was introduced to the system operating according to TL (i.e., stochastic factor of 0), then the mean α value of TL was at the expected theoretical value of 1, regardless of growth rate. However, when the size of the stochastic factor was increased to be > 0, TL's α value changed from 1 to a higher or lower value based on the vine growth rate. For simulations when the population was declining, an increase in the stochastic factor led to a decrease in the α value. On the other hand, for simulations when the population was increasing, an increase in the stochastic factor led to an increase in the α value. This matches the expectations of a system operating under the LC model of stochasticity (Cohen et al., 2016), suggesting that our deviation from the theoretical value of TL was expected, given stochasticity in our system. Thus, we could conclude at this point that the vines growing on our Puerto Rican coffee farms was growing according to the TL and LC models, as noted by Cohen and colleagues (2016).

With this initial conclusion, another piece of the puzzle that we had to figure out was the range of our empirical α values. While our system was operating under a LC model that was subcritical (i.e. the intrinsic growth rate of increase, r, was below 1), and thus had α values below 1, the wide range of our values (Table 1 and Figure 4) was still confusing. In trying to understand this range, we looked at how we had been modelling our simulations. In our simulations, we had been using a small sample size (less than 20) of coffee farms (which could also be interpreted as individual coffee plants), as this was close to our actual data. We decided to increase our simulation size both spatially and temporally, i.e. using 100 farms instead 12, and using 100 time periods instead of 12 (Figure 5), controlling for stochasticity.
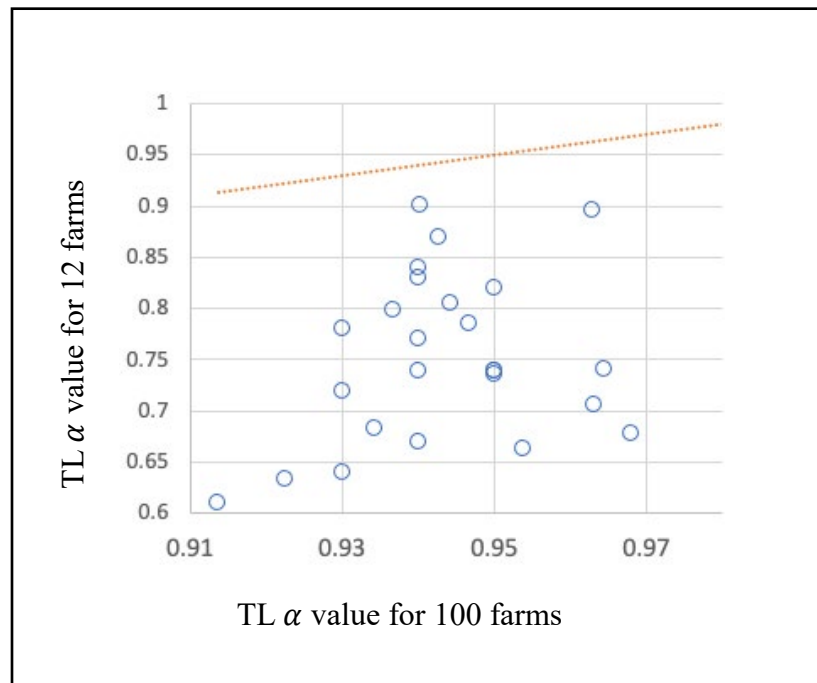

Figure 5: Comparison of α values of simulations of Taylor's Law for 12 farms (close to sample size) versus 100 farms. Stochastic factor is set to zero. Dashed red line indicates one to one relationship.

As seen in Figure 5, in the simulations using only 12 farms, the range of the α values was approximately 0.6 to 0.9. In contrast, the simulations using 100 farms had α value ranges from 0.91 to 0.97. Thus, even with no stochasticity, when the LC model predicts that the α value of TL should be at 1, the simulation with a smaller number of farms had α values far below 1. In comparison, the simulation with a larger sample size more closely followed the LC model. So it appears that the deviation from a TL parameter of 1 in the empirical data may have also been a consequence of small sample size, for both time and space, to be in line with the expected α value for our system operating under the LC model. In conclusion, it seems that Taylor's Law is present in the vine coverage on the sampled Puerto Rican coffee farms. However, the deviations in the empirical α values can be attributed to both the Lewontin-Cohen model of stochasticity where the community of vines are declining over time and space on average, and the fact that our empirical data was from a small sample size in both space and time.

The final piece our puzzle was seen in Table 1, where one of the farms, LASM3, had very low R^2 values with 11% and 38% variance explained at spatial and temporal scales respectively. This particular farm had been abandoned since our last visit, and overgrown with a single particular invasive vine species, the potato vine (*Dioscorea bulbifera*). We propose that the failure of this farm to fall in line with TL is related to the dominance of this one vine species taking over this particular coffee farm.

Conclusion

This paper is an attempt to intertwine the fields of theoretical ecology and agroecology, suggesting that relatively simple ecological laws can be used to understand agroecosystems and gain insights for the management of these systems. The main aim of our research was to test for the presence of such an ecological law, Taylor's Law, in an agricultural context, the management of vines, regarded as weeds, on coffee farms. Through this, our main question was whether the spatial and temporal forms of Taylor's Law was present in the vine coverage on coffee plants in Puerto Rican coffee farms. Our research leads us to the conclusion that not only are both forms of Taylor's Law present, but that other statistical and ecological forces were at play.

We found that the coverage of vines on coffee bushes on sampled coffee farms not only followed the expectations of Taylor's Law with a high R^2 value and a consistent α value, but also that our α value was lower than the theoretical expected value of 1. We conclude that this disparity between expected and actual TL parameter in both the temporal and spatial forms results from added stochasticity, as suggested by the Lewontin-Cohen model of stochastic growth. Furthermore, our lower than expected α value could be caused by the Lewontin-Cohen model being subcritical, which is to say the average growth rate of vines is negative. In addition, we also found that our sample size of 22 farms over 12 months was insufficient to capture the full α value of our study system. Thus, a combination of Taylor's Law, the Lewontin-Cohen model, and sample size were at play within our research. We hope that the results of this study will eventually be informative as ecological weed management systems are developed by Puerto Rican coffee farmers.

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